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**ELEMENTS OF  
PLANT BIOLOGY**

*by Lancelot Hogben*

PRINCIPLES OF ANIMAL BIOLOGY

*Drawings by G. J. F. Horrabin*

# ELEMENTS OF PLANT BIOLOGY

by

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*Illustrated*

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## PREFACE

This does not claim to be a new book either in outlook or method; it merely seeks to bring up to date the *Elements of Plant Biology* first written by Professor Tansley in 1922 and revised by the present author in 1935. I have not hesitated to retain a few paragraphs *verbatim* where redrafting seemed pointless; but it has been necessary to take into account so much new material that an almost complete rewriting was felt to be essential. For this reason, Professor Tansley has preferred that his name should no longer appear on the title page, but the original title is retained with his permission. The responsibility for this attempt to modernise a text that has already had a long period of useful service must rest solely with the author. Some expansion of scope has been found necessary, and it is hoped that the fundamentals of botany have been presented in a form suitable for senior classes in schools and preliminary classes in colleges and universities.

I am deeply indebted to my colleagues in the Oxford Department of Botany for much valuable advice and information, and particularly to Miss Pamela Grant for making the great majority of the drawings.

Several publishers have kindly given permission for the reproduction of certain figures, and it is a pleasure for me to make formal acknowledgement.

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Figs. 136a and 216a-c from *Introduction to Botany*, by Priestley and Scott (Longmans, Green & Co., Ltd.).



# CONTENTS

<i>Preface</i>	v
I. INTRODUCTORY: PLANTS AND ANIMALS	1
Living and not living. Cellular structure of living matter. Differences between plants and animals. Relations of animals and plants to energy. The naming and classification of plants and animals. Range of form and structure in the plant world.	
II. SIMPLE ORGANISMS: <i>AMŒBA</i> . <i>PROTOCOCCUS</i> AND <i>EUGLENA</i>	17
<i>Amæba</i> : Structure. Movement. Nutrition and excretion. The contractile vacuole. Irritability. Growth and reproduction. Encystment. <i>Protococcus</i> : Nutrition and excretion. <i>Euglena</i> : Movement. Nutrition and excretion. Irritability. Contractile vacuole. Reproduction. Encystment. Comparison of <i>Amæba</i> , <i>Protococcus</i> and <i>Euglena</i> .	
III. SOME PHYSICAL CHARACTERS OF ORGANIC SUBSTANCES	31
Crystalloids and Colloids. Colloidal phases. Lyophobic sols. Lyophilic sols. Microscopic, ultramicroscopic and submicroscopic particles. Internal surface of colloids. Surface energy and adsorption. Gels. Diffusion and dialysis.	
IV. PROTOPLASM AND THE CELL	41
Protoplasm. Cells and the cell doctrine. Cell walls. Intercellular substance and intercellular spaces. The plant cell. Parenchyma. Meristematic cells. The nucleus. Mitosis. Division of the chromosomes and the doctrine of permanence. Cell division; the formation of new walls. Development of the adult parenchyma cell. Water relations of the cell. Turgor.	
V. THE GREEN CELL: PHOTOSYNTHESIS	64
Chlorophyll and chloroplasts. Chlorophyll and light. External factors affecting photosynthesis. The stages of photosynthesis. Products of photosynthesis. Formation of starch in the chloroplasts. Significance of photosynthesis.	
VI. ORGANIC SUBSTANCES AND THEIR CHEMICAL CHARACTERS	72
Inorganic constituents of protoplasm. The carbohydrates. Sugars. Monosaccharides: glucose and fructose. Disaccharides: maltose and sucrose. Polysaccharides. Fats. Proteins. Other organic substances. Enzymes.	
VII. PLANT METABOLISM: RESPIRATION	85
Synthesis and anabolism. Digestion. Aerobic respiration. Plant oxidations. Anaerobic respiration. Respiration of succulent plants. Respiration of fat-storing tissues. Energy changes during respiration. Respiration in plants and animals.	



VIII. THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA	95
<p>"Immortality" of unicellular organisms. <i>Chlamydomonas</i>: structure. Nutrition. Asexual reproduction. Formation of gametes. Sex differentiation. <i>Pandorina</i>: reproduction. <i>Eudorina</i>: reproduction. <i>Volvox</i>: reproduction. The soma in plants and animals. The filamentous algæ. <i>Ulothrix</i>: reproduction. <i>Spirogyra</i>. Cell division. Reproduction. Nature and significance of sexual differentiation. Isogamy, anisogamy, oogamy.</p>	
IX. DIFFERENTIATION OF TISSUES: <i>FUCUS</i> , THE SEA-WRACK	124
<p><i>Fucus</i>. Microscopic structure of the thallus. Nutrition and conduction. Sexual reproduction. Development of the young plant. Adaptation to the intertidal zone.</p>	
X. THE SIMPLEST LAND PLANTS: <i>PELLIA</i>	139
<p>The aquatic ancestry of land plants. <i>Pellia</i>. Structure of the thallus. Growth of the thallus. Reproduction. Sporogonium. Liverworts and mosses.</p>	
XI. ALTERNATION OF GENERATIONS: <i>DRYOPTERIS</i>	148
<p>Zygosis and meiosis. Alternation of generations. <i>Dryopteris filix-mas</i>: the sporophyte. Spore formation. Gametophyte. Antheridia. Archegonia. Embryology. Adaptation of the fern to land life.</p>	
XII. HETEROSPORY: THE LIFE HISTORY OF <i>SELAGINELLA</i>	160
<p>Pteridophyta. <i>Selaginella</i>: habit. The cone. Microsporangia. Male gametophyte. Megasporangia and female gametophytes. Fertilisation.</p>	
XIII. THE SEED PLANTS: THE LIFE HISTORY OF <i>PINUS</i>	168
<p>Microsporangiate cones. Male gametophyte. Megasporangiate cones. Pollination. Female gametophyte. Fertilisation. The seed.</p>	
XIV. THE FORMS AND LIFE HISTORIES OF THE FLOWERING PLANTS	178
<p>Monocarpic and polycarpic plants. Exposed plants. Surface plants. Half-hidden plants. Hidden plants. The erect herbaceous annual. Perennials. Runners. Rhizomes. Tubers. Corms. Bulbs. Bulbils. Perennation, multiplication and spreading.</p>	
XV. TISSUE ELEMENTS OF THE SEED PLANTS	197
<p>Secretory cells. Storage cells. Surface cells. Conducting cells. Mechanical cells. Pits. Materials of the cell wall. Lignification. Cutinisation. Suberisation. Mucilage formation.</p>	
XVI. THE GROWING POINT OF THE SHOOT	213
<p>Apical meristem. Leaf primordia and axillary buds. Development behind the shoot meristem. Elongating region of the stem.</p>	

CONTENTS		ix
<b>XVII. THE FOLIAGE LEAF: TRANSPIRATION</b>	Form. Structure. Mesophyll. The veins. Epidermis. Transpiration. Wilting. Significance of transpiration.	221
<b>XVIII. THE PRIMARY STEM</b>	Structure. Structure of a young internode. The monocotyledonous type. Maintenance of the erect position.	233
<b>XIX. THE PRIMARY ROOT: ABSORPTION OF WATER AND SALTS</b>	The root system. Growing point of the root. The elongating zone. Root-hair formation. Structure of the primary root. Origin of lateral roots. Primary root structure of monocotyledons. Absorption of water. Uptake of nutrient salts. Nutrient elements obtained from the soil. Deficiency signs. Modified roots.	245
<b>XX. WOODY PLANTS: TRANSLOCATION</b>	Forms of trees and shrubs. Secondary meristems. Secondary thickening. Secondary rays. Annual rings. Sapwood and heartwood. Cork formation. Bark. Abscission layers. Secondary thickening in roots. Translocation.	260
<b>XXI. GROWTH, DEVELOPMENT AND IRRITABILITY</b>	The growth cycle. Vernalisation. Photoperiod. Nutritional factors. Correlation. Growth hormones. Irritability. Taxis. Nastic movements. Tropisms.	281
<b>XXII. THE FLOWER</b>	Inflorescences. Parts of the flower. Insect pollination. <i>Ranunculus acris</i> : perianth, andræcium, gynæcium. Wind pollination. <i>Thalictrum minus</i> : perianth, andræcium, gynæcium. Development of pollen. Development of the ovule. Development of gametes and fertilisation.	292
<b>XXIII. SEEDS AND FRUITS</b>	The seed. Development of the fruit. Dry, indehiscent fruits. Dehiscent fruits. Succulent fruits. False fruits. Dispersal by wind. Dispersal by animals. Dispersal by water carriage.	306
<b>XXIV. GERMINATION</b>	Dormancy and viability. Conditions for germination. Enzyme formation and activity. Rupture of the seed coat. Structural changes. Use of seeds by man. Death rate and competition.	315
<b>XXV. HEREDITY AND EVOLUTION</b>	Heredity. Mendel's hypothesis. Mendelian ratios. Dominance. Inheritance of two pairs of characters. Linkage. Pure lines. Heterosis. Genes and chromosomes. Meiosis. Evolution. Morphological evidence. Historical evidence. Geographical evidence. Selection and breeding. The method of evolution. Origin of new varieties. Mutation. Hybridisation. Natural selection. Survival of sexual reproduction. Fitness and adaptation.	324

XXVI. YEAST	340
Structure. Habitats. Nutrition. Metabolism. Life cycle. Utilisation of yeasts.	
XXVII. BACTERIA AND VIRUSES	346
Size and structure of bacteria. Movement and response to stimuli. Nutrition. Photosynthetic bacteria. Chemosynthetic bacteria. Saprophytic bacteria. Parasitic bacteria. Respiration and synthesis. Fermentation. Reproduction. Spore formation. Dispersal. Sterilisation. Pure cultures. Species and strains. The circulation of nitrogen. Putrefaction. Nitrification. Nitrogen fixation. Pathogenic bacteria. Viruses. Bacteriophage. Viruses and vegetative propagation: loss of vigour.	
XXVIII. THE FUNGI	362
Saprophytic fungi: the moulds. <i>Mucor</i> . Spore formation. Chlamydospore formation. Conjugation. Heterothallism. Parasitic fungi. Methods of control. <i>Peronospora</i> . Asexual reproduction. Sexual reproduction. Symbiotic fungi: mycorrhizas. Ectotrophic mycorrhiza of <i>Pinus</i> . Endotrophic mycorrhiza of <i>Calluna</i> . Vitamins. Antibiotics.	
SPECIAL REAGENTS	375
INDEX	376

## Chapter I

# INTRODUCTORY PLANTS AND ANIMALS

Biology<sup>1</sup> is the science of living beings or organisms, and botany<sup>2</sup> is that part of biology specially concerned with plants. Green plants are very literally the staff of life, because they are the only agents that transfer matter and energy from the non-living, inorganic world into the living and organic. Animals, and nearly all the colourless plants, can feed only on organic materials made by plants that are green. The study of plants teaches us some things about life that we cannot learn, and others which we cannot so easily learn, from the study of animals. It is therefore worth while for any who want to acquire a knowledge of biology as a whole, and not only for specialists in botany, to learn something about plants. It may not be necessary for non-specialists to gain the detailed and comprehensive knowledge that the botanist has to acquire, and their studies should be directed rather to what plants can teach them about life as a whole than to a knowledge of them for their own sakes. The title of this book is intended to emphasise this point of view. But it must be clearly understood that a foundation of value to more advanced studies, or to a general education, cannot be obtained merely from a book alone, but must be sought at the laboratory bench and in the field also.

### *Living and Not Living*

There is usually little practical difficulty in deciding whether common objects are alive or not. We realise that a living being, such as a man, possesses many characteristics not shared by minerals and stones. But when we try to express the difference in the formal terms of a definition great difficulty arises. A complex organism is not necessarily all alive or all dead. Old trees contain much inert wood; and

<sup>1</sup> From the Greek βίος (bios), life.

<sup>2</sup> Greek βοτάνη (botanē), plant or pasture, connected with βόσκω (boskō), to pasture, feed.

although a man dies when the heart stops beating, the hair continues to grow for some time longer. No single characteristic will sharply distinguish living from non-living materials. Living matter and what we call life are unique on account of the sum of their properties, not on account of any single one of them. They may be briefly summarised as follows: Living matter is unstable and is always undergoing *continuous internal changes*, revealed externally by the gaseous exchanges of respiration. Even in the dormancy of seeds and winter

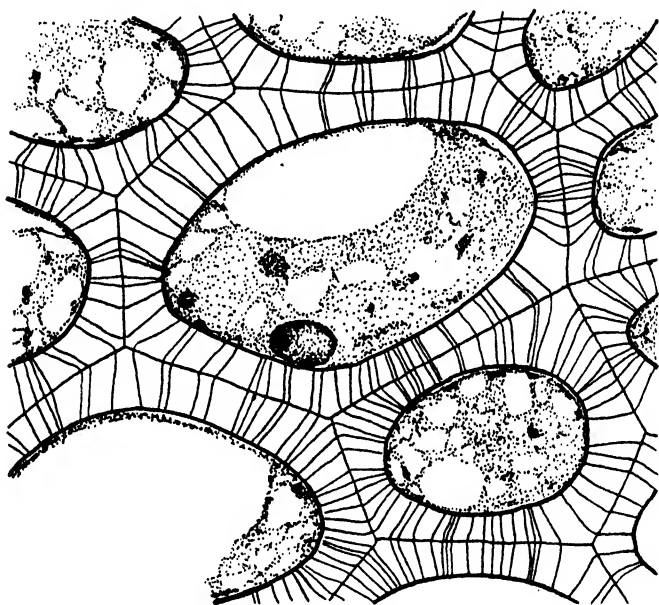


FIG. 1.—Cells from the ripe seed of *Diospyros ahenii*, showing protoplasmic fibrils passing through thick cellulose walls,  $\times$  about 800. After Quisumbing.

buds there are the slow reactions of maturation. *Irritability*, or the property of responding to a wide range of external influences, is very marked. Some inanimate substances may react to special external factors—the photo-electric cell responds to light by producing an electric current—but it is characteristic of living matter to respond to many. *Assimilation*, i.e. the power of taking in foreign substances and converting them by chemical and physical changes into its own structure, produces *growth*, which is also a fundamental property of living matter. Growth is discontinuous, and is interrupted by *reproduction*, which has little real analogy among non-living things. There

is no non-living system in which so complicated and delicately adjusted a unity can maintain itself and assimilate new material to itself in the way that living matter does.

### *Cellular Structure of Living Matter*

When we come to examine their structure with the microscope, we find that the bodies of nearly all plants and animals are composed of what are called cells and of the products of cells. Plant cells are usually the more easily recognisable as such, because each is surrounded and separated from its neighbours by a cell wall of non-living substance. The living substance, or *protoplasm*, lines the more readily visible walls and is the material in which all the ultimate life-processes occur. Whole and undivided it is alive; but any attempt to separate its numerous constituents results in its death. A large part of the adult plant body consists of non-living organic substances formed by the protoplasm. These include the cell walls which form a kind of "skeleton," assisting rigidity. The protoplasm is generally continuous from cell to cell by means of exceedingly fine filaments which, even under the microscope, can only be seen after the wall has been artificially swollen. They pass through the cell walls in great numbers (Fig. 1) and all, or nearly all, the protoplasm of the plant really forms a single connected structure. This is sometimes called the *symplast*.

The protoplasm of many of the cells of the higher plants disappears during the life of the plant, and only their dead walls remain. This occurs extensively in the outer bark and heartwood of tree trunks, which are themselves dead, though they are integral parts of the living plant body, just as the finger-nails are part of a living man.

### *The Differences between Plants and Animals*

The most familiar plants and animals are those which are highly developed and complex. In their very different fashions they are closely adapted to their environments and ways of life, and are sharply distinct. The higher plants are rooted in one place, they are green, or at least have green leaves, they branch freely and so have loose and spreading forms, which go on extending as long as they remain alive. The higher animals, by contrast, are freely motile, they are variously coloured, have compact bodies and complete their growth while still young. All these differences can be related to a fundamental difference in feeding habits. Plants absorb substances which are in a high state of dispersion as gases or aqueous solutions. The higher animals can take solid food into the body and

bring it into solution. The substances absorbed by plants are chemically simple and widely distributed in low concentrations in the air and in fertile soils. The food of animals is chemically very complex and often scattered so that enough could not be obtained by a wholly sedentary organism. Thus the diffuse habit of plants, both above and below ground, is closely related to their absorption of gaseous carbon dioxide from the air and inorganic salts from the soil solution. It provides large areas of contact between the plant and its nutrient surroundings. So loosely knit a structure could only be immobile; and absorption and growth are slow, more or less continuous, and prolonged.

Plants are green, or have green parts, because of the green colouring matter, *chlorophyll*.<sup>1</sup> Its possession is, with rare exceptions, the character which enables plants to build up their bodies from simple inorganic substances. This formation of organic compounds from inorganic, by the agency of chlorophyll, requires the presence of light, and is called *photosynthesis*.<sup>2</sup> *The continuance of life upon the earth depends on photosynthesis, because it is the only process which makes new organic substance on a large enough scale.*

Animals do not possess this power. They feed upon organic products of vegetable photosynthesis. Their motility is associated with the necessity to seek them out, and their compactness is in turn related to the requirements of moving bodies. It is made possible by the organisation round an internal gut in which digestion of the solid food is accomplished. The many other differences of structure and organisation which distinguish the higher animals and the higher plants are all related, directly or indirectly, to the fundamental difference in the substances they absorb. It should clearly be appreciated, however, that this is only to say that plants and animals have developed along two different structural and functional lines. It says nothing of what is cause and what effect. The nature of the relations between form and function in living things is often very difficult to understand, and nothing is gained by making crude guesses where evidence is lacking.

There are both plants and animals that depart in one respect or another from the general characters listed above. *Tapeworms* are examples of parasitic animals which do not move about but remain fixed to the membrane of their host's intestine. They have no

<sup>1</sup> "Leaf-green" from Greek *χλωρός* (*chlōros*), green and *φύλλον* (*phullon*), a leaf.

<sup>2</sup> "A putting together with the help of light," from Greek *φῶς* (*phōs*), *φωτός* (*phōtos*), light and *συνθεσις* (*sunthesis*), putting together.

mouth or gut, and absorb suitable food all over their surface. The food is already partly digested by the host and is always organic. There are groups of insectivorous plants, of which the sundews

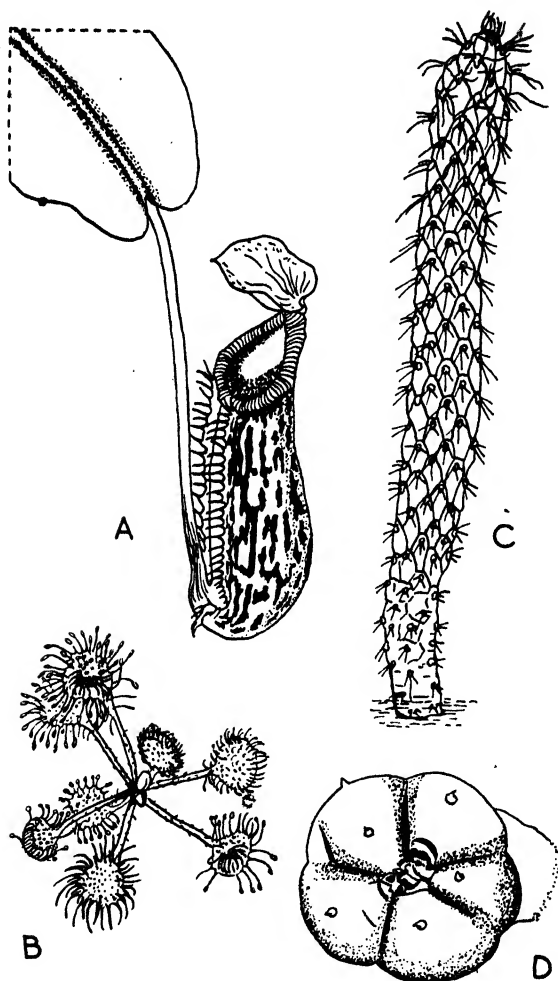


FIG. 2.—A, pitcher of *Nepenthes* sp. B, plant of *Drosera rotundifolia*. C, young plant of *Opuntia cylindrica*, a cactus. D, young plant of *Gymnocalycium hossei*, also a cactus. All  $\times 2/3$ .

(*Drosera*) and pitcher-plants (*Nepenthes*) are good examples, able to consume solid food. The sundews trap small insects on their sticky, glandular leaves (Fig. 2 B) and the pitcher-plants drown them



in the depths of their bag-like leaves (Fig. 2 A). The solid remains are dissolved by fluids excreted from the leaf surfaces, and the organic matter thus digested passes into the body of the plant. It does not form the sole nourishment of such insectivorous plants, which possess normal methods of plant nutrition as well. Animals such as *coral polyps* build fixed and branching colonies, though they have a distinctively animal type of nutrition, and *cactuses* (Fig. 2 C and D) have compact, unbranching bodies, though otherwise they are typical plants.

There are simple, microscopically small, organisms living in water which have some animal and some plant characteristics. They resemble some of the organisms produced early in the history of life and they have not become differentiated like the higher organisms, the unmistakable familiar animals and plants. Thus there is a minute oval organism called *Chlamydomonas* (Fig. 41, p. 98) which lives in pools. It is green and takes in only dissolved salts and gases like a plant, but during most of its life it swims actively about like an aquatic animal. It must be reckoned as a plant; because, as we saw, the mode of feeding is the basal character of difference, but it still retains the animal character of free locomotion. There are other minute organisms which feed in both ways, partly on dissolved and gaseous substances, partly on solid food; and these escape the meshes of any definition of an animal or plant.

*We cannot, in fact, frame any comprehensive definition which will sharply separate all living organisms into animals and plants.* This conclusion illustrates a truth that the student will realise more and more fully as his biological studies progress, namely, that it is useless to expect the facts of nature exactly to fit our definitions, however carefully framed. There are so many different ways in which living substance may take shape, so many varieties of function, i.e. ways in which it may work, and so many possible combinations of both of these, that there are certain to be exceptions to every rule we try to lay down. But that does not mean that we have to give up the task of analysing and classifying form and function, or the science of biology would be impossible. We can always recognise *types of structure* and *types of function* to which organisms conform more or less closely, because their physical and chemical constitution forces them, so to speak, along certain lines of differentiation and behaviour. Only we must not expect to draw sharp lines. The forms included in any of the groups we make will usually tend to shade off into forms belonging to other groups.

Thus we can say that the essential animal character depends upon the habit of consuming solid organic food; that the essential plant character depends upon the habit of absorbing gases and inorganic salts in solution; that a man is indubitably an animal, while an oak tree is as indubitably a plant; that with the man we can group a host of other different kinds of organisms as animals and with the oak tree a host of other organisms as plants; but that when we come to minute microscopic organisms we find the differences, which are so clear and sharp among the higher forms, becoming blurred, till finally we arrive at forms of which it is impossible to assert that they are definitely animals or definitely plants.

### *Relations of Animals and Plants to Energy*

The essential difference between animals and plants in their relation to food determines also their characteristic difference in relation to energy. All living organisms change energy from one form to another—actually to many others. The radiant energy of sunlight is converted to the electrochemical energy binding organic molecules together; which in its turn is converted to the energy of motion and electric potentials; to heat, and even back to light. Here we must note the broad difference between animals and plants: it is that *animals consume organic food and reduce free energy by producing much heat and doing work; while plants in the main build organic substance, increasing the free energy of their world more than they reduce it.* And since life, or at least its more obvious dynamic attributes, consists in the expenditure of energy, animals live more intensely than plants and react to more varied stimuli, i.e. to influences which lead to their expending energy in various ways. But because they are alive, plants do spend (i.e. decrease free) energy and are sensitive to many stimuli (cf. p. 285). The shoots of a plant grow and bend, for example, towards the light, and its roots towards a source of water. Conversely, animals store energy in organic substances such as fat and glycogen, and so have a reserve that will carry on their active life without fresh food for a time.

### *The Naming and Classification of Plants and Animals*

The immense multitudes of individual plants and animals existing on the earth are exceedingly varied in form and structure, and in order to get any understanding of plant or animal life we must *classify* them in some way. We recognise at once—mankind has recognised from the earliest times—that there are many different

*kinds*, but of these some resemble each other so closely that they are difficult to distinguish, and can only be separated by those who have made a special study of the forms in question, while others are very distinct indeed. For instance, a blackberry is obviously different from



FIG. 3.—*Rubus fruticosus* L., the blackberry; a flowering shoot.  $\times 2/3$ .

a raspberry in the colour and taste of the fruit, and in the fact that the former has hard prickles which can tear the flesh while the latter has soft prickles which can only irritate it. But there are many different kinds of blackberry, some of which differ from one another in such small and variable characters that even specialists who have

spent a large part of their lives in studying the blackberries do not agree exactly how they should be grouped.

We allot individuals that breed together and resemble one another more or less closely to a single *species*, but authorities differ as to what they consider species, and there is not yet agrément as to whether the conception of a species can be made at all precise. Species which are most like each other are grouped into *genera*, and genera which are most like each other into *families*. Thus the raspberry and the blackberry are different species of one *genus*, the sweet briar and the dog rose, of another genus belonging to the same *family*. The hare



FIG. 4.—*Rubus idæus* L., the raspberry; a flowering shoot.  $\times 2/3$ . Note the similarity of the flowers and fruits to those of Fig. 3. After Sowerby.

and the rabbit are different species of one genus; the dog, the wolf and the fox of another belonging to quite a different family, though to the same large group, the mammals, which include all animals that suckle their young, comprising such diverse types as rats and mice, elephants, whales and men.

The standardised nomenclature which is used in naming the different botanical<sup>1</sup> species we recognise, and which enables us to record and systematise them, gives each genus a Latin name—a noun—and adds a qualifying adjective or adjectival noun, for the species. To avoid ambiguity, and because occasionally the same name has accidentally been given by different investigators to different organ-

<sup>1</sup> Zoological practice differs in some minor respects.

isms and different names to the same organism, an indication of the "authority" for the name is often added. Thus while the genus to which both the blackberry and the raspberry belong is called *Rubus*, the blackberries, if we lump them all together as one species, are *Rubus fruticosus*<sup>1</sup> L. (Fig. 3); and the raspberry is *Rubus idæus*<sup>2</sup> L. (Fig. 4); the L. standing for Linnæus. Small, but apparently constant, differences which are not regarded as important enough to establish a separate species, are given rank as a variety. Thus the sweet briar is *Rosa eglanteria*<sup>3</sup> L. It has a number of varieties, one of which is named *Rosa eglanteria* var. *rotundifolia* Reichb.<sup>4</sup> from its small, rounded leaves. Both the above genera, along with many others, belong to one family, the *Rosaceæ* or rose family,

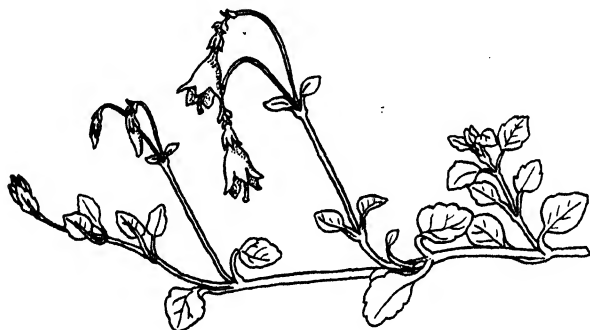


FIG. 5.—*Linnea borealis*.  $\times 2/3$ . After Sowerby.

because they have certain characteristics of the flower and fruit in common. The *Rosaceæ* are united in their turn with some score of other families, into the order *Rosales*, a large group embracing a considerable range of floral structure, but still within recognisable limits and different, for example, from those of the *Ranales* or buttercup order.

Very many species have no common names in any language because they have not impressed their existence on man by their usefulness or harmfulness or conspicuousness—they have not, in fact, attracted his attention in any way—until botanists and zoologists began to study them for their own sake. Linnæus, who named so

<sup>1</sup> Latin, *fruticosus*, shrubby.

<sup>2</sup> *Idæus*, belonging to Mount Ida.

<sup>3</sup> Latinised from Eglantine, French name of this species.

<sup>4</sup> Heinrich Gottlieb Ludwig Reichenbach, German botanist, 1793–1879. These "authorities" are given as examples. It has not been thought necessary to give them throughout the book.

many plants and animals, chose to have such a plant named after him *Linnea borealis* (Fig. 5). The Latin nomenclature has the indispensable advantage of being international, at least in the way it is written. Its use in biology is, in fact, a relic of the time when Latin was the universal language of learning.

### *Range of Form and Structure in the Plant World*

The plant kingdom in its entirety may be parcelled out into a number of divisions or phyla, some of which differ so widely from the familiar flowering plants that they possess no conspicuous organs comparable with flowers, and may escape the attention of the ordin-

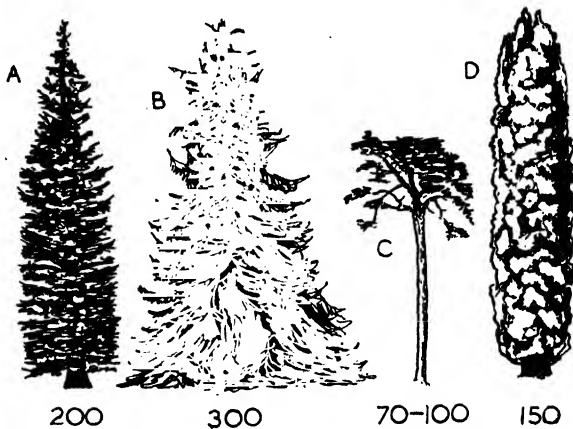


FIG. 6.—Gymnosperms. A, *Abies magnifica*, Californian red fir. B, *Pseudotsuga douglasii*, Douglas fir. C, *Pinus sylvestris*, Scots pine. D, *Libocedrus decurrens*, incense cedar. The figures below each are normal heights in feet.

ary flower lover altogether. Starting with the familiar seed plants, the main divisions are as follows :

1. **SPERMAPHYTA**, the seed-bearing plants, comprise two main classes: (a) the *Angiosperms*, or true flowering plants, which bear their seeds in fully enclosed structures, the fruits, that develop from flowers usually rendered conspicuous by their bright envelopes. They include all the familiar herbs, shrubs and broad-leaved trees. (b) The *Gymnosperms*, which bear their seeds not fully enclosed but between the scales of cones. They include all the needle-leaved pines, firs and similar evergreen trees (Fig. 6). The Spermaphyta all have a highly elaborated and complex internal structure; the most advanced to be found among plants.

2. **PTERIDOPHYTA**. These possess stems, roots and leaves like the Spermatophyta with well-developed internal structure. They do not reproduce their kind by seeds, but by simpler, minute bodies called *spores*. The most familiar plants of this division are the ferns (Fig. 7 B-E); but the clubmosses (e.g. *Selaginella*, p. 160) and the horse-tails (Fig. 7 A) also belong. These last are few and small, and repre-

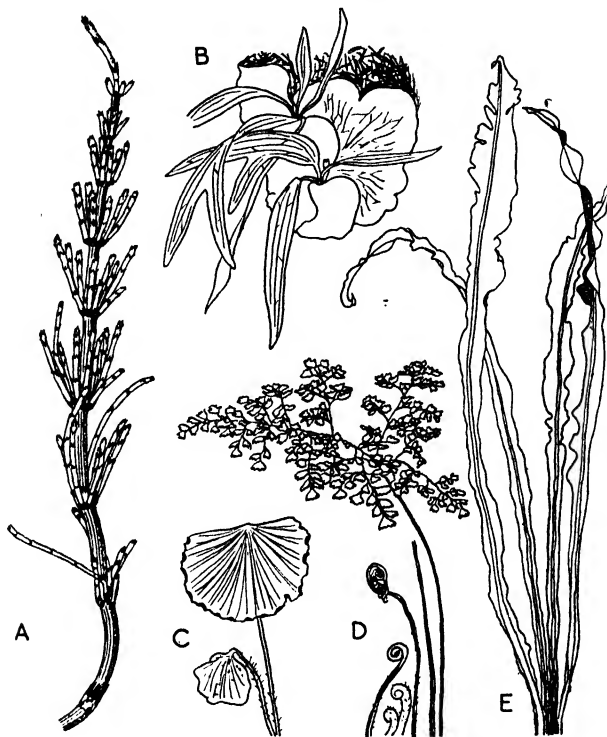


FIG. 7.—A, young shoot of *Equisetum arvense*.  $\times \frac{1}{2}$ . B, *Platycerium* sp.  $\times \frac{1}{10}$ . C, *Adiantum reniforme* fronds.  $\times \frac{1}{3}$ . D, *Adiantum cuneatum*.  $\times \frac{1}{4}$ . E, *Polypodium irioides*.  $\times \frac{1}{8}$ .

sent the descendants of a phylum formerly much more important. Their ancestors are preserved in the coal measures and other rocks and attained the size of large trees. In the same rocks are preserved plants intermediate between the Pteridophytes and Seed Plants, the Pteridosperms, with the habit of ferns and reproduction by seeds, but seeds very different in structure from those of existing spermatophytes.

3. **BRYOPHYTA**, including mosses and liverworts (Chapter X), also reproduce by spores. They are, generally speaking, smaller and

much less highly organised than Pteridophytes. Their internal structure is simple. The mosses and some of the liverworts have simple stems and leafy laminæ, but many liverworts have no differentiation of this kind, the plant body consisting of a flat strap or ribbon-shaped structure of indefinitely continued growth. Such a plant body is termed a *thallus* (Fig. 8 A).

4. ALGÆ. Unlike the previous divisions, these plants are mostly unable to live in air, and occur in sea and fresh water at varying depths, but mostly near the surface. They all contain chlorophyll, but their green colour may be masked by additional brown and red pigments. They may be unicellular like *Chlamydomonas* (p. 97), or filamentous like *Spirogyra* (p. 115), or may attain to a thallus with a fair degree of internal organisation like *Fucus* (p. 124). Other algæ mentioned in this

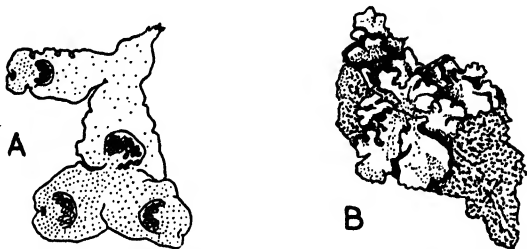


FIG. 8.—A, *Lunularia*, a liverwort with strap-shaped thallus and detachable fragments (gemmae). B, thallus of a lichen growing on a piece of bark.  $\times 2/3$ .

book are *Protococcus* (p. 21), *Volvox* (p. 108) and *Ulothrix* (p. 113).

5. FUNGI possess about the same grade of organisation as the algæ, ranging from microscopic yeasts (p. 340) through moulds and mildews to bulky mushrooms and toadstools (Fig. 9). Since they possess no chlorophyll, they are colourless or occasionally varicoloured, and depend on organic food.

6. LICHENS are peculiar compound plants consisting of algal and fungal species living together in a single thallus. The thallus of lichens may resemble that of liverworts in a general way, but it has a range of colours. Lichens form their encrustations on exposed wood and stones of all sorts (Fig. 8 B).

7. PROTISTA include the bacteria (p. 346), the smallest of all organisms visible under the microscope. They are mostly colourless and many have the animal character of locomotion, but they are plant-like in other respects. The protista also include many other groups of simple organisms in which plant and animal characters are not separated. *Euglena* (p. 22) is an example.

8. VIRUSES resemble bacteria in many of their manifestations; but they are smaller and will usually, though not always, pass



through unglazed porcelain filters that keep bacteria back. They are generally too small to be visible even under a microscope. Like some of the bacteria, they are known mainly from the diseases that they cause in plants and animals. Some have been extracted and outside the host they do not show living characteristics. They are on the border line of the living and non-living.

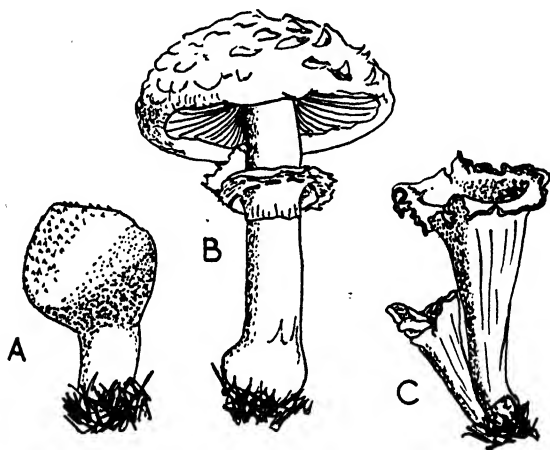


FIG. 9.—Fungi with bulky fruiting bodies. A, *Lycoperdon perlatum*. B, *Lepiota procera*. C, *Craterellus cornucopioides*. The vegetative part of the fungus is underground. All  $\times 2/3$ .

In the series outlined above we have descended from bulky and complex plants living mostly on land and getting water from the soil, to ever simpler forms increasingly dependent upon a watery medium. The simplest algæ are microscopic and live wholly submerged in ponds or the sea; while the viruses are submicroscopic and can exist only in the body fluids of the host. It is an established biological dictum that the higher plants living on dry land have gradually arisen, during the history of the world, from simpler plants confined to water. This is an application of the idea of *organic evolution* (Chapter XXV) to plants, a doctrine of whose truth Darwin was the first to succeed in convincing the world.

## Practical Work

### A. THE MICROSCOPE AND ITS USE

The microscope is used by biologists more than any other instrument. The strict observation, from the outset, of a few simple rules will keep it in good adjustment and increase the ease and efficiency of the student using it.

Wipe the lenses only with a soft handkerchief and polish the slide and coverslips before use. Keep the lenses free from liquids and wipe them clean at once if they are wetted by accident. Objects lying on the slide may be examined with the low power; but a coverslip must always be put on before the high power is used. Focus *downwards* and with care or the preparation may be crushed. Always locate the object with the low power and then turn over to the high. Never slope the microscope, but work with the microscope stage horizontal so that the slide need not be clipped but can be freely moved. Lift only by the handle incorporated in the frame, never by the tube.

The eye not looking down the microscope may be kept *open*. A very little practice will overcome the initial awkwardness and will be well rewarded in avoiding eye strain.

(1) Starting from bench-level, identify the *mirror*, *substage diaphragm* and *condenser*, *objectives*, *tube*, *coarse* and *fine focusing adjustments* and *eyepiece*. Learn the use of these parts.

(2) Put a drop of water on a slide and cover with a coverslip, including a number of air-bubbles in the droplet. Examine under low and high power objectives. With the high power, focus slowly downwards and note carefully the changing appearance of the bubble as the focal plane descends.

(3) Mount a single moss leaflet in a drop of water, put on a coverslip, being careful *not* to include any air-bubbles, and examine under the low and high powers. When using the high power, note carefully and draw the appearance of a single cell when the objective is focused upon (a) the top, (b) the mid-line and (c) the bottom of the cell. From such a series of optical sections a better idea of the cell structure can be obtained. How are the green chloroplasts placed in relation to the transparent walls? What occupies the centre of the cell?

(4) An appreciation of the real and relative sizes of microscopic objects is of great importance to a proper understanding of them. If stage and eyepiece micrometers are available, the student should calibrate his microscope, determining the magnitude at stage level which corresponds with one division of his eyepiece micrometer. This should be done for both low and high powers. Most low powers (one-third inch focal length) magnify about 100 diameters and most high powers (one-sixth inch focal length) magnify about 450 diameters. If micrometers are not provided, these may be regarded as approximate values for the microscope used. Drawings should *always* be labelled with at least the approximate magnification. Experience will teach the value of this.

#### B. TYPES OF THE PLANT KINGDOM

(5) Note the superficial characters of the divisions of the plant kingdom as represented by a series such as the following. *Angiosperms*, any flowering annual; *Gymnosperms*, a branch of pine or fir, bearing cones; *Pteridophyta*, a complete fern plant, with spores; *Bryophyta*, a moss; *Algæ*, a green pond scum; *Fungi*, a mushroom, toadstool or bread-mould; *Lichen*, from an old wall or tree-trunk; *Bacteria*, rotten hay or pea infusion; *Virus*, crinkled potato leaf or "aucuba" tomato leaf.

The choice of material may be readily adjusted to suit place and season.

#### C. DIFFERENCES BETWEEN SPECIES OF THE SAME GENUS

(6) Examine carefully fresh specimens of three species of flowering plants belonging to the same genus. Write down (a) the differences and (b) the similarities which strike you.

The following speedwells are suitable in April:

*Veronica agrestis* L., *V. hederifolia* L., and *V. tournefortii* Gmel. (= *V. buxbaumii* Ten. = *V. persica* Poir.).

The following buttercups in May or June:

*Ranunculus acris* L., *R. repens* L., and *R. bulbosus* L.

The following oaks in autumn:

*Quercus robur* L., *Q. sessiliflora* Salisb., *Q. ilex* L.

#### D. EXCEPTIONS TO THE CHARACTERISTIC FORMS OF PLANTS AND ANIMALS

(7) A BRANCHING ANIMAL. Fresh or museum specimens of a hydroid polyp or a bryozoon "colony." Each individual has a mouth surrounded by tentacles and a gut. It consumes solid food consisting of tiny organisms living in the sea, and is therefore an animal in spite of the fact that it is fixed to one spot and that the whole "colony" has a branching form like a plant.

(8) A COMPACT PLANT. *Mammillaria*, or other cactus from subtropical America, shows no obvious division of its shoot into stem and leaves. It has a branching root in the soil, like an ordinary plant, but its shoot consists of a compact fleshy green stem bearing spines or bristles.

(9) AN ANIMAL WITH NO MOUTH. The tapeworm is a parasitic animal which absorbs its liquid organic food from the intestines of the animal in which it lives. It has no mouth or gut, having lost these by degeneration in correspondence with its habit of life.

(10) A PLANT WHICH CONSUMES SOLID FOOD. The sundew (*Drosera*) and the pitcher plant (*Nepenthes*) are insectivorous plants which digest and absorb the products of insects that fall on to the leaf or into the pitcher (a modified part of the leaf). This is a character not possessed by most plants, but it serves to demonstrate the common powers of plant and animal protoplasm. In other respects the sundew and the pitcher plant are ordinary flowering plants.

## Chapter II

### SIMPLE ORGANISMS

#### AMŒBA, PROTOCOCCUS AND EUGLENA

##### AMŒBA

*Amæba* provides convenient material for the direct study of protoplasm. It is a minute, unicellular animal and there are several species. *Amæba proteus* and others live in fresh-water pools and are to be found on the surface of the mud or on water plants. *Amæba limax* is marine. Each individual consists of an irregular speck of protoplasm 100–250  $\mu^1$  across. *Amæbae* placed in a shallow glass dish on a black background are just visible to the naked eye as light grey dots. Most of the following details are visible by direct

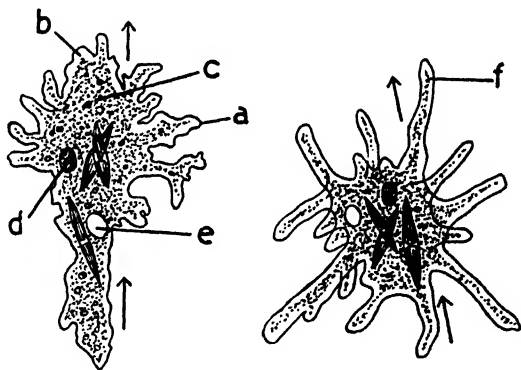


FIG. 10.—*Amæba proteus*. Two successive views of the same individual. The arrows show the direction of movement. *a*, plasmalemma; *b*, ectoplasm; *c*, endoplasm; *d*, nucleus; *e*, contractile vacuole; *f*, pseudopodium. The spindle-shaped bodies are diatoms (unicellular algæ), that have been taken in as food.  $\times$  about 200. After Cash.

inspection under the high power of the microscope; but a few need special methods of preparation to bring them out.

##### Structure

An *Amæba* (Fig. 10) is a naked mass of protoplasm and has no cell wall secreted round it. Its surface is bounded, however, by a rela-

<sup>1</sup> $\mu$ , symbol for micron = 1/1,000 of a millimetre.

tively tough and solid gel membrane, the plasmalemma<sup>1</sup> about 0.25  $\mu$  in thickness. Immediately inside this is a clear layer, the ectoplasm.<sup>2</sup> The greater part of the organism, the endoplasm,<sup>3</sup> appears granular, due to the presence of crystals, oil globules and other inclusions of all sizes down to the limits of visibility. In the endoplasm is a disc-shaped body, the nucleus, an all-important part of the protoplasm found in all living cells. If an *Amæba* is cut in two, the half with the nucleus survives. Both parts cover themselves with a normal surface; but the half without a nucleus is unable to feed and soon exhausts its resources and dies. The endoplasm also contains a number of relatively large vacuoles and minute vacuoles or alveoli. In general the term *vacuole* is applied to almost any bright and clear inclusion of the protoplasm. The clearness is not, however, due to its emptiness; but to its being filled with a clear solution.

### Movement

The most obvious thing that *Amæba* does is to move. When the animal is active its shape continually changes, owing to the slow appearance of projections, called pseudopodia<sup>4</sup> (Fig. 10 f). In *Amæba proteus*<sup>5</sup> several pseudopodia may form at a time, but in *A. limax*<sup>6</sup> only one, and the organism flows along rather like a microscopic slug (Fig. 11 A). As the pseudopodium is formed in one direction, the protoplasm at the further side is withdrawn, and it can be seen fairly easily that the included granules of the central endoplasm, the plasmasol, are flowing forwards into the pseudopodium. No return flow is usually visible along the outer layers, which appear to be of a firmer gel consistency (the plasmagel) (Fig. 11 Ab); except perhaps at the extreme tip of the pseudopodium (Fig. 11 Aa). As the plasmagel remains attached to the plasmalemma and so to the substratum, there is slow progress in the direction of the pseudopodium. The plasmasol flows continuously through a tube of plasmagel which is simultaneously built up ahead and liquefied behind. This type of protoplasmic movement has something in common with that inside plant cells. The outer layers of plant protoplasts remain attached to the cell walls and rotation of the inner layers can be seen to carry the granules and other inclusions with it. Since there is no

<sup>1</sup> Greek *πλάσμα* (plasma), thing moulded; *λίμμα* (lemma), thing peeled off.

<sup>2</sup> Greek *ἐκτός* (ectos), outside.

<sup>3</sup> Greek *ἐνδον* (endon), within.

<sup>4</sup> Greek *ψευδός* (pseudo), false; *πούς*, *ποδός* (pous, podos), a foot.

<sup>5</sup> The name *Amæba* is derived from Greek *αμοιβή* (amoibe) change; *proteus* from the Latin demi-god Proteus fabled to have the power of changing himself into any form.

<sup>6</sup> Latin, a slug.

deformation of the plant cell wall, as there is of the amœboid plasma-lemma, no movement of the organism as a whole results. The rate of movement of *Amœba* is of the order of  $1\ \mu$  per second, so that the organism travels its own length in about three minutes. The rate in-

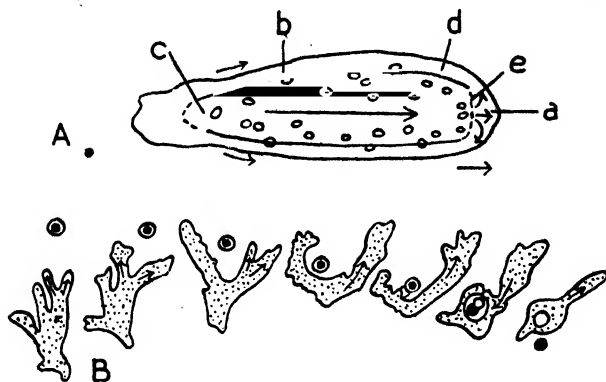


FIG. 11.—A, *Amœba limax*; a, fluid ectoplasm; b, plasmagel; c, endoplasm; d, gelating ectoplasm; e, layer beyond which endoplasmic granules do not advance. After Pantin; diagrammatic. B, stages in ingestion of a particle of food, arrows showing direction of flow of the protoplasm. Time, 8 minutes. After Schæffer.

creases with temperature up to  $20\text{--}30^{\circ}\text{C}$ ., and slowly comes to a standstill in the absence of oxygen. It is also prevented by dilute cyanide, a respiratory poison, and a connection between respiration and movement seems clear.

### Nutrition and Excretion

The streaming movement of the pseudopodia is also important in the method by which *Amœba* feeds. When a pseudopodium touches another small body, such as a unicellular plant or a colony of bacteria, the protoplasm flows round it or draws it into the body (Fig. 11 B). There is some difference in the ease with which different substances are taken in. Proteins, and hence other unicellular organisms, are absorbed readily; fat globules and quartz particles less easily, if at all. A drop of water is taken in with the ingested prey, and the sac thus created is a food vacuole. Into this, enzymes (p. 81) are secreted which break down, i.e. digest, the solid materials into soluble forms which pass into the protoplasm and are assimilated. The non-digestible parts are left behind as fæces by the flowing away of the protoplasm and the reformation of the plasmalemma behind the extruded body. This process of defæcation is sometimes loosely

called excretion, but it differs from the excretion of soluble waste products formed during the chemical breaking down of food materials in respiration. The fæces are the rejected materials which have not suffered chemical decomposition. True excretion occurs all over the surface of an *Amæba* into the external water. Carbon dioxide and uric acid (from nitrogenous foods) are among the materials known to be excreted.

### *The Contractile Vacuole (Fig. 10 e)*

Situated in the ectoplasm and bulging into the endoplasm is a clear spherical space which can be seen slowly to increase its size and then quite suddenly shrink and disappear. It slowly reappears in the same position, and it is evident that a quantity of liquid is being alternately collected and expelled. The protoplasm retains numerous soluble materials and water is therefore driven into it by osmosis (p. 58). If entry continued indefinitely the protoplasm would swell and finally burst. Instead of this happening, the entering water collects in the contractile vacuole and is returned by its contraction to the outside. This forcing of water out of the protoplasm against the osmotic gradient involves the transformation of energy which is provided by respiration. How this comes about is uncertain. Soluble materials in the water will be expelled along with it from the organism, but it has not been possible to show the presence of much nitrogenous waste matter in the contractile vacuoles of *Amæba* and similar organisms. The main substance excreted by them is the water itself. *Amæba limax*, that lives in sea water with an osmotic pressure similar to the cell contents, does not have a contractile vacuole.

### *Irritability*

*Amæba* is sensitive to external stimuli and its movements are directed in relation to such stimuli. For instance, its protoplasm streams away from a source of heat when the temperature rises towards 35° C. At 0° C. and at 35° C. the pseudopodia are withdrawn and the animal becomes spherical and motionless. The same thing happens if it is suddenly subjected to bright light—as during microscopic examination. *Amæba* is also sensitive to the presence of food, and it has been shown that cells of this type encounter slightly soluble particles more frequently than is dictated by mere chance; whereas completely insoluble substances, such as quartz particles, are contacted only at random. This probably means that when the low concentrations of soluble materials diffusing from the slightly

soluble particle come into contact with the surface of the *Amæba*, they affect the direction of its movement, which then proceeds up the concentration gradient to the particle itself. Similar *chemotaxis* occurs in the movements of fern sperms towards the egg and in many other motile cells.

### *Growth and Reproduction*

By the formation of new protoplasm from ingested materials, *Amæba* adds to its bulk and grows in size so long as assimilation exceeds the breaking-down processes resulting in excretion. When the growth of the individual has reached a certain limit it divides into two. The nucleus first divides into two equal parts; and then a furrow appears in the protoplasm and rapidly deepens till the two halves become entirely separate. This simple method of multiplication is called binary fission. Each of the halves is a complete *Amæba* in every respect and each proceeds to live its own independent life and ultimately grows to the size of the parent *Amæba* when it divides again in the same way.

### *Encystment*

Occasionally reproduction takes a rather more complicated form. Under unfavourable conditions an *Amæba* may withdraw all its pseudopodia, become rounded off, and form a resistant casing or cyst around itself. In this state it will withstand freezing or drying up, and may be blown about as a particle of dust and so be distributed from one place to another. Inside the cyst division into two or even several daughter cells may take place, and the encystment thus becomes a method of reproduction as well as of distribution and protection.

## PROTOCOCCUS

*Protococcus viridis*<sup>1</sup> Ag. (= *Pleurococcus vulgaris* Naeg.) is found everywhere in the temperate zones. Its cells form a thin greyish-green crust on the bark of trees, old palings and the like, especially on their moister and shadier side. In dry weather this coating becomes dried out and crumbles under the point of a knife. The cells are very resistant to desiccation; but in this dried state their activity is very much reduced. If a little of the green crust is scraped off into a drop of water and examined under the microscope it will be seen to consist of numerous very small cells about 10–20  $\mu$  in diameter. Each cell (Fig. 12) is bounded by a colourless cell wall of firm con-

<sup>1</sup> Greek *πρωτος* (prōtos), first; *κοκκος* (kokkos), berry and Latin *viridis*, green.



sistency. Inside this is the protoplasm. Under the low power this may appear uniformly green; but under the high power the colour is shown to be restricted to a lobed chloroplast embedded in the protoplasm and lining the wall. By appropriate staining the central nucleus may also be distinguished, but it is generally hidden by the highly coloured chloroplast. There is no vacuole.

*Protochoccus* reproduces itself by cell division, the nucleus dividing first and then the chloroplast; a delicate wall is afterwards formed across the cell, separating it into two halves (Fig. 12 e). A single free

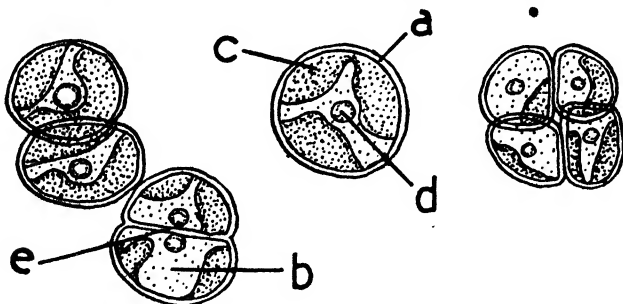


FIG. 12.—*Protochoccus viridis*. a, firm cell wall; b, central cytoplasm; c, chloroplast; d, nucleus; e, cross-wall of new division.  $\times 500$ .

cell is usually more or less spherical, but very frequently the cells remain grouped together, with flattened sides where they touch, for some time after division. All stages of cell division and separation are frequently to be seen.

#### Nutrition and Excretion

*Protochoccus* forms its body from carbon dioxide, water and minute amounts of nutrient salts. The last are provided by the moisture trickling down the supporting post or tree, and the carbon dioxide comes from the surrounding atmosphere. No solid food is able to pass the resistant cell wall. Excretion of carbon dioxide from respiration and absorption of oxygen go on all over the surface as in *Amæba*; but there is no extrusion of solid particles and the cells are completely non-motile.

#### EUGLENA

*Euglena*<sup>1</sup> *viridis* Ehrenb. is found in stagnant water, sometimes in such quantity as to colour it green. It is particularly abundant in water containing much nitrogenous matter, such as the drainings

<sup>1</sup> Greek *eu* (eu), typical; *γλήνη* (glênē), puppet.

from dung heaps. It is spindle-shaped and about  $50\mu$  long. The forward end is blunt and is furnished with a thin prolongation of the protoplasm, a flagellum,<sup>1</sup> almost as long as the cell itself (Fig. 13 a). The flagellum passes along the side of an infolding (Fig. 14 E) called the gullet, and is continued into a more or less spherical cavity, the reservoir, to the bottom of which it is attached. At one side of the reservoir is a contractile vacuole which may be surrounded by a ring of smaller vacuoles (Fig. 13 b). Near by is a red spot called the stigma<sup>2</sup> (Fig. 13 c). There is a nucleus towards the centre or the pointed hinder end, with a fairly conspicuous nucleolus. Embedded in the protoplasm are a number of green chloroplasts (Fig. 13e) radiating from a common centre, and scattered granules of paramylum, a polysaccharide resembling glycogen (p. 78).

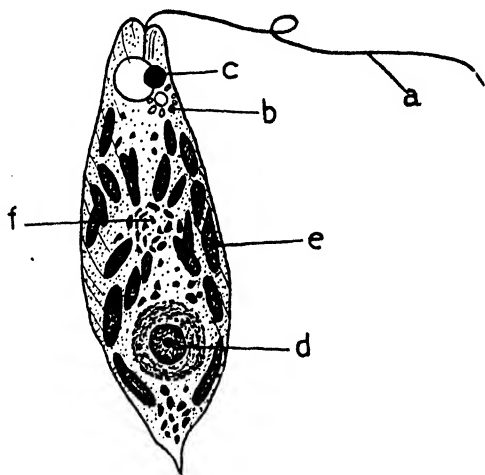


FIG. 13.—*Euglena viridis*. a, flagellum; b, contractile vacuole surrounded by ring of smaller vacuoles; c, stigma; d, nucleus; e, chloroplast; f, paramylum granules.  $\times$  about 1000. After Doflein, modified.

### Movement

*Euglena* is surrounded by a firm outer membrane. It does not put out

pseudopodia and, although it shows some changes of shape due to simultaneous contraction of one part of the cell and expansion of another (Fig. 14 A–D), it does not depend upon them for its movements. This results from the activity of the flagellum which is apparently not a mere appendage of the protoplasm but a self-supporting part of it that can go on producing movements even when separated from most of the cell, including the nucleus. At the attached end of the flagellum is a deeply staining “basal granule” just inside the cell surface. At the time of cell division an obvious thread also extends from the basal granule to the nucleus (Fig. 17), but this disappears

<sup>1</sup> Latin, a little whip.

<sup>2</sup> Greek *στίγμα* (stigma), a mark or spot,

in the mature stage of the cell. A free-swimming *Euglena* normally carries the flagellum in a somewhat reflexed position (Fig. 16 A) which makes it rather difficult to observe closely as it gets hidden by the body of the cell. The movement of the cell is caused by waves that pass along the flagellum, generated by the activity of the flagellar protoplasm itself. They are dependent on its oxygen respiration and come to a stop in the absence of oxygen or in the presence of dilute cyanide. As in *Amæba* and in the muscles of the higher animals, activity is not stopped immediately by the absence of oxygen; the cells can incur an "oxygen debt," but must sooner or later be returned to air or perish.

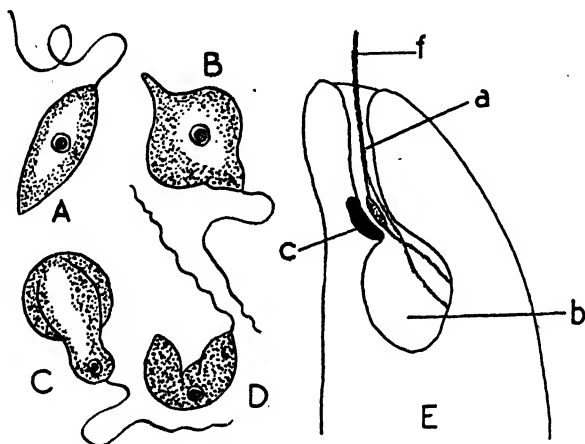


FIG. 14.—*Euglena*. A–D, changes of shape due to expansion and contraction within the firm membrane. After Kent & Klebs. E, anterior end of *Euglena viridis*. a, gullet; b, reservoir; c, stigma; f, flagellum.  $\times$  about 2000. After Wager.

The waves pass along the flagellum, starting at the base and increasing their amplitude (Fig. 15) and also their velocity as they travel out towards the tip in a spiral. The increasing energy exhibited must come from the flagellum itself. The rate of the beat is dependent on temperature and oxygen supply, but is usually about twelve to the second. As the cell moves forward it can be seen to rotate and gyrate so that the path of any spot near its anterior end would appear as Fig. 16 B, if seen from ahead. The positions of the *Euglena* cell during one complete rotation and gyration, taking approximately one second, are represented in Fig. 16 C. The spiral wave-beats of the flagellum, approximately twelve times as frequent as the rotation and gyration of the cell, cause the twelve vibrations indi-

cated in Fig. 16 B. Since the impulses are constantly changing their direction, they cause the front end of the cell (and hence the cell as

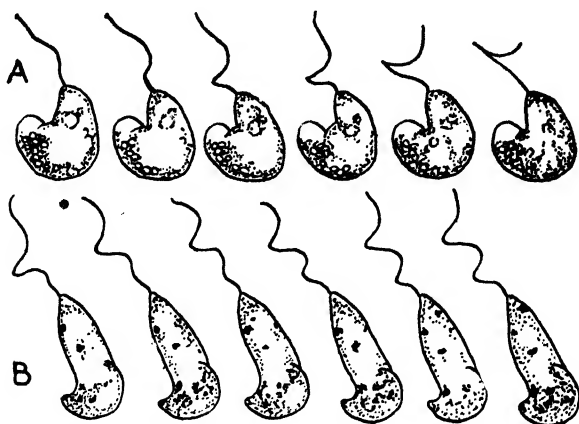


FIG. 15.—*Peranema trichophorum*. A, (left to right) a wave passing along the flagellum from base to tip with increasing amplitude, B, a second wave starting from the base behind the first. After photographs by Lowndes.

a whole) to rotate and gyrate as actually observed. Together with the forward component this constitutes a corkscrew motion. The

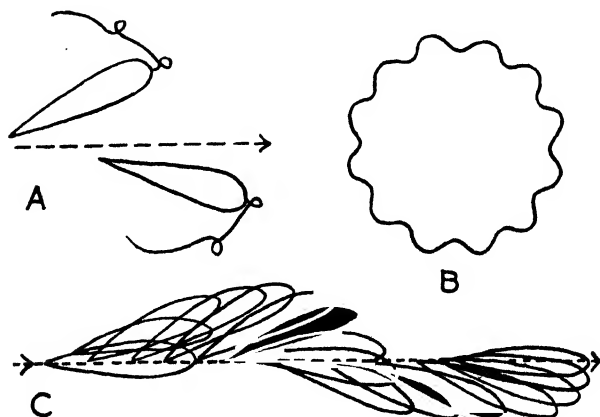


FIG. 16.—A, position of the flagellum and direction of movement in a free-swimming *Euglena*. B, see text. C, positions taken by a *Euglena* cell in passing through one complete rotation and gyration, as seen from the side. Flagellum omitted. After Lowndes.

reason for the forward movement is easy to understand when the flagellum is reflexed as it usually is in *Euglena viridis*. It has been observed that, even if the flagellum is carried at right angles to the cell body, a forward movement of the cell occurs, and this is believed to be due to the "vortex" resulting from the gyrations. Water is not displaced backwards but instead the cell moves forwards. A strong swimmer has found that he can move rapidly forward under water merely by rotating his arms to create such a "vortex." The rate of forward movement of *Euglena* is about 100–200  $\mu$  per second, or about 2–4 times its own length. This is about 100 times faster than the movement of *Amæba* and, under the high power of the microscope, is fast enough to make it difficult to retain the moving organism in the field of vision. But it has to be remembered that the micro-

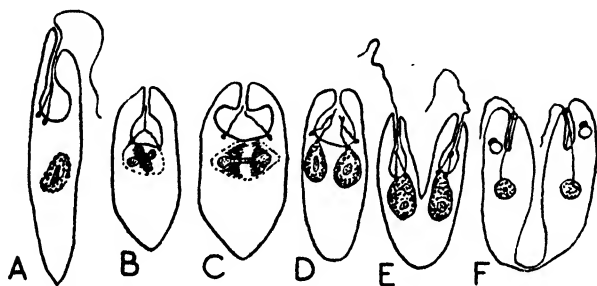


FIG. 17.—A–E, stages in the division of *Euglena gracilis*. Mitosis (p. 51) is occurring in B and C. Note the connection between flagellum and nucleus. After Krichenbauer. F, late stage of division in *Euglena viridis*. After Storer.

scope magnifies space only and not time; so that an altogether false impression of velocity results. The *Euglena* rate is about 1/10,000 of human walking speed. Similarly although the flagella appear to be vibrating at high speed, they are not really capable of rapid movement, and no large organism depends for its movement upon flagella.

### Nutrition and Excretion

As *Euglena* has chloroplasts it can elaborate carbohydrates from carbon dioxide dissolved in the water around it, i.e. it possesses a plant, or *holophytic*,<sup>1</sup> type of nutrition. Soluble salts and oxygen for respiration pass in and soluble waste products pass out over the entire surface. Since it occurs most abundantly in water rich in

<sup>1</sup> Greek *ὅλος* (holos), entire; *φύτον* (phuton), plant.

decaying organic matter, *Euglena* probably also absorbs soluble organic food through its outer surface—a type of nutrition called *saprophytic*.<sup>1</sup> Holozoic nutrition, the absorption of solid particles, as by *Amæba*, does not seem to occur in *Euglena viridis* but is believed to occur by way of the reservoir in some allied organisms.

### *Irritability*

*Euglena* moves towards a source of moderate light; but away from a high intensity. The sensitivity to light is believed to be associated with its absorption by the red pigment in the stigma. Similar “eye spots” are found in many motile unicellular organisms (cf. *Chlamydomonas*, p. 99) and are absent from the non-motile.

### *The Contractile Vacuole*

*Euglena* possesses a small contractile vacuole situated beside the reservoir. Several minute vacuoles in a group can sometimes be seen to empty themselves into the main vacuole (Fig. 13 b) which in turn discharges its fluid into the reservoir. Its function is probably similar to that of the vacuole of *Amæba*, viz. the removal of excess water forced into the organism by osmosis.

### *Reproduction*

Active *Euglenæ* reproduce frequently by binary fission in the direction of the long axis (Fig. 17). The nucleus first performs mitosis (i.e. equal division by the mechanism described on p. 51). Then the other parts of the cell, the flagellum, reservoir, contractile vacuole and so on are duplicated. When the daughter nuclei have separated to opposite sides of the cell, a cleavage furrow appears at the anterior end between the two reservoirs and works backward until cell division is completed.

### *Encystment*

*Euglena* may also lose its flagellum, become non-motile and form a thick carbohydrate coating or cyst especially when strongly illuminated. Inside the cyst successive divisions may occur until 16 or 32 daughter cells have been formed. In some species there may be no division inside the cyst, which is then purely a means of surviving unfavourable conditions.

<sup>1</sup> Greek σαπρος (sapos), decayed.

*Comparison of Amæba, Protococcus and Euglena*

Some of the more important of the observable similarities and differences between these three simple organisms are listed in the following table.

	<i>Amæba</i>	<i>Protococcus</i>	<i>Euglena</i>
Pigment . . .	None	Chlorophyll	Chlorophyll
Nutrition . . .	Holozoic	Holophytic	Both Holophytic and Saprophytic (Holozoic?)
Cell wall . . .	None	Present	None
Shape . . .	Variable	Fixed	Somewhat variable
Motility . . .	Pseudopodial	None	Flagellate
Vacuole . . .	Contractile	None	Contractile

*Amæba* and *Protococcus* are typical animal and plant cells respectively (cf. p. 3). The fundamental distinction appears to lie in the lack or possession of chlorophyll and in the method of feeding that results. In *Euglena*, a member of the Protista, this criterion breaks down; *Euglena* possesses chlorophyll but fails to develop a cell wall, utilises additional methods of nutrition and is motile. A further interesting comparison may be made with *Chlamydomonas* (p. 97) which resembles *Euglena* in most respects detailed above, but forms a firm wall.

Many thousands of unicellular organisms have been observed and described. Many of them are much more complex than the simple types described above (Fig. 18). Their boundless diversity defies any rigid classification and illustrates the protean variety of protoplasm.

## Practical Work

### A. OBSERVATION AND DRAWING OF STRUCTURE

Accurate drawing of the structures observed is an essential in biological studies. It is not merely a way of recording work done, but an indispensable means of training the mind to form and retain clear mental pictures. There is no substitute. Do not be discouraged if you are not naturally adept with the pencil; a little determination and horse sense will enable anyone to acquire the very moderate degree of skill needed. The following rules will help and should be strictly observed from the outset.

Use a pencil of medium hardness and keep a fine point on it. Press lightly. Use plain paper with a hard surface.

Draw on a scale large enough to be able to show all the desired details clearly.

Begin with clear outlines. Do not tolerate vagueness. Use little shading and

never shade until the outlines are accurate. In drawing from the microscope shading is very rarely helpful.

Draw only what you actually see; but remember that seeing comes with practice.

Always label your drawing; i.e. write the names of the parts of what you draw at the side and join with an indicator line.

Show the appropriate magnification at the foot of the drawing.

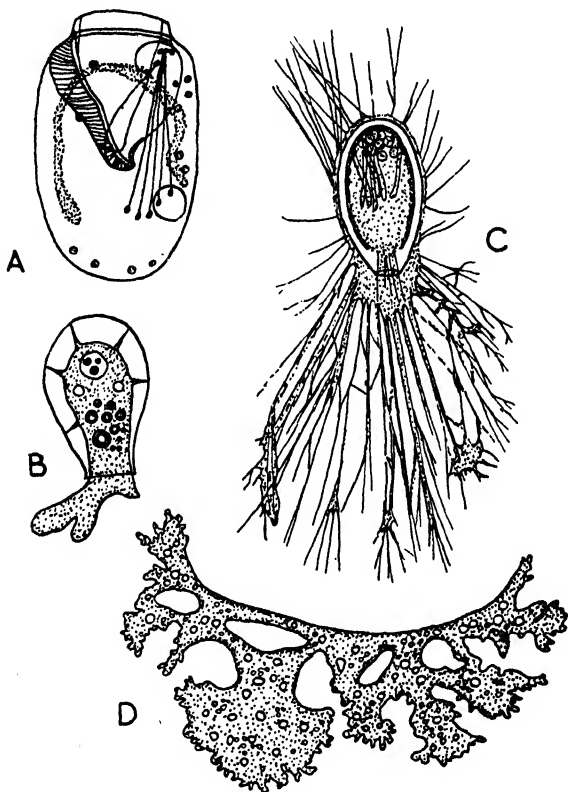


FIG. 18.—A–C, complex unicells. A, *Euplotes* sp. B, *Hyalosphenia lata*, similar to *Amœba* but forming a shell of chitin. After Lang. C, *Gromia*, the protoplasmic fibrils ingest food particles and there is a chitinous shell embedded in the body of the protoplasm. D, plasmodium of *Licea pannorum*.  $\times 66$ . After Cienkowski.

#### B. AMŒBA—A SIMPLE ANIMAL

(1) Place a drop of water containing one or two *Amœbæ* on a slide. Examine with the low power and pick out the *Amœbæ* as irregular greyish blobs. Put on a coverslip very carefully and gently. Remember that *Amœba* is a fluid sol and readily dispersed. Examine with the high power and notice that it is slowly changing its shape. Note the *pseudopodia*.

Distinguish the *ectoplasm* from the *endoplasm*, and note that the granules of



the latter are very various in size and shape. Fragments of ingested prey may be visible in the endoplasm.

Identify the *contractile vacuole* and watch its movements. Locate the *nucleus*.

(2) Make a series of outline drawings showing successive forms assumed as a *pseudopodium* is put out or withdrawn. See if you can observe the ingestion of a particle of food.

(3) Run a little iodine solution under the coverslip and i-rigate it through by placing a piece of blotting paper or filter paper at the opposite side. The iodine will "fix" the *Amæba* by coagulating its proteins. The *nucleus* may stain more deeply than the cytoplasm and so become more easily visible.

(4) If available, examine a permanently mounted specimen of *Amæba* stained to render the inclusions more conspicuous.

NOTE.—*Amæbae* are to be found in the scrapings from rotting leaves and other detritus round the edges of ponds, but are often very scarce. When obtained, they may be multiplied and maintained more or less indefinitely as follows. Put a dozen wheat grains into about half a litre of water, boil for five minutes and then cool. Introduce as many *Amæbae* as possible into this medium together with a few drops of the water in which they were found. Some of the *Amæbae* may be expected to establish themselves and multiply. To maintain the culture prepare fresh fluid and transfer the *Amæbae* every other month. Keep warm in cold weather. *Amæbae* may also be obtained from the usual agencies.

#### C. PROTOCOCCUS—A SIMPLE PLANT

(5) Scrape a little of the green crust from the surface of a tree or paling. Disperse a small amount in a drop of water on a slide. Put on a coverslip and examine under the low power. Note the numerous green specks and clusters. Put on the high power and distinguish the *cell wall*, *chloroplast* and colourless *cytoplasm*. The nucleus will probably be hidden by the chloroplast. If there is a bright granule, the *pyrenoid*, included in the chloroplast, it indicates that the cell belongs to the allied organism *Trebouxia*.

(6) Observe clusters of cells showing stages of *cell division*; (a) when the new cell is not yet formed but the chloroplasts of the daughter cells are distinct, and (b) when thin cross walls have appeared.

#### D. EUGLENA—A MEMBER OF THE PROTISTA

(7) Place a drop of water containing *Euglena* cells on a slide and cover. Note the firm *outer membrane*, the *chloroplast* and the *reservoir* at the anterior end. Note also the disturbance caused by the *flagellum*. Look for the *eye spot* at the side of the reservoir. If the movement is too rapid for accurate observation run a little iodine under the coverslip and, when this has taken effect, look for the *nucleus*, *nucleolus* and granules of *paramylum*.

## Chapter III

### SOME PHYSICAL CHARACTERS OF ORGANIC SUBSTANCES

#### *Crystalloids and Colloids*

A solid substance when brought into contact with water behaves in one of several ways. It may react chemically with the water; like sodium, which breaks up the water molecule, combining with the oxygen and liberating hydrogen. Alternatively it may dissolve to form the solute of a *true solution*, disappearing as it does so. It is characteristic of a true solution that the solute is dispersed as free molecules (e.g. in a sugar solution) or as ions (e.g. in a salt solution) throughout the solvent. The individual particles, whether molecules or ions, act independently very much like the molecules of a free gas. As another alternative, the solid substance may remain practically unaltered, like grains of sand. If, however, the coarse grains are reduced in a very finely grinding mill into finer and finer particles, a degree of fineness is reached at which the particles stay suspended in water for an appreciable length of time before settling out. Such a system is called a suspension. Suspensions slowly separate or "break," the dispersed phase sinking to the bottom, if heavier, or rising to the top if lighter than the dispersing liquid.

If the grinding of the solid particles can be carried still further they will ultimately be reduced to a size at which they no longer separate out from the dispersion liquid at all, but form a stable system known as a *colloidal sol*.<sup>1</sup>

Particles of all these sizes are present together in soil. If we stir up a handful in a beaker of water the coarser and heavier sand particles sink to the bottom at once, others (silt) sink more slowly; but the very fine colloidal particles (clay) form a sol, and the salts go into true solution.

Colloidal systems can thus be designated as those whose dispersed particles are larger than isolated molecules and smaller than those of

<sup>1</sup> From Greek κολλα (kolla), glue. Glue forms a sol when heated with water.

a suspension. Few molecules attain a diameter of  $1\text{ m}\mu$  and the colloidal size-range may roughly be said to run from  $1\text{ m}\mu$  to  $1\mu^1$ ; but it must be realised that there is no sharp division at these arbitrary limits. A few large molecules, such as those of starch, and the proteins exceed  $1\text{ m}\mu$  diameter, and such substances form sols with water, but not true solutions. Many substances with smaller molecules can be induced by different methods of preparation to form true solutions with fully dispersed molecules and colloidal sols in which clusters of their molecules are aggregated. They may thus exist in either the crystalloidal or colloidal condition. Usually a decided preference is shown for one state or the other. Substances which most readily form true solutions are loosely termed *crystalloids* (because many of them also form crystals) and those which most readily form sols are called *colloids*. Sugar and salt are typical crystalloids and starch, gelatine, glue and clay are typical colloids.

### *Colloidal Phases*

Every colloidal system must contain two phases, the *continuous* sometimes also called the dispersion medium, and the substance dispersed in it, called in the aggregate the *dispersed phase*. The dispersed phase does not necessarily consist of solid particles and the continuous phase of a liquid, as in the examples already described. Any combination of two phases in a suitable degree of dispersion constitutes a colloidal system. Fog (liquid in gas); foam (gas in liquid); ruby glass (solid in solid) are all examples; but the systems important in the constitution of living matter are solid in liquid (suspensoids) and liquid in liquid (emulsoids). The dispersion medium is almost always water, or more accurately water containing a small amount of dispersed substance in true solution. Just as relatively coarse solid particles suspended in water form a suspension and tend slowly to separate, relatively coarse liquid droplets form an emulsion, and tend to sink or rise to the surface according to their specific gravity. Thus, on shaking up chloroform and water an emulsion may easily be formed which slowly breaks into layers of chloroform below and water above. The fat globules suspended in milk, on the other hand, slowly rise to the surface as cream, leaving the watery skim milk below. Suspensions and emulsions fall just outside the colloidal range, but are frequently encountered in biological materials.

<sup>1</sup> $\mu$  = micron, the thousandth part of a millimetre. It is the ordinary unit of microscopic measurement.  $\text{m}\mu$  denotes millimicron, the thousandth part of a micron and  $1/1,000,000$  mm. It is the unit of ultramicroscopic measurements. Molecules are commonly measured in Ångstrom units (Å);  $10\text{Å} = 1\text{ m}\mu$ .

### *Lyophobic Sols*

Colloids can be classified according to the physical state of the two constituent phases. Their properties and behaviour are to some extent determined by the nature of the two phases; but even more markedly by the relationship between them. Some colloids are easily separated into their two phases, e.g. by centrifuging or by flocculating the disperse phase by the addition of small amounts of a precipitating agent such as salt. They are termed *lyophobic*<sup>1</sup> colloids. Suspensoids, such as the purple sols obtained by means of a submerged arc between gold electrodes, are typical. Lyophobic colloids owe such stability as they possess to two causes. The first is the continual erratic movement of their particles, known as Brownian movement from its discoverer.<sup>2</sup> It results from the unequal impact of molecules of the liquid dispersion medium upon the colloidal particles. As the size of the particles is reduced gravitational fall becomes less and Brownian movement greater. At a diameter less than  $1\ \mu$  (colloidal dimension) the two become equal and sedimentation is indefinitely prolonged. The second cause of stability is afforded by any electrical charge upon the particles causing mutual repulsion. It is, for example, impossible to prepare a stable electro-neutral gold sol, but if a small amount of electrolyte is added, the ions become attached to the surface of the gold particles and render the sol stable. Gold sols of this type prepared by Faraday (1791–1867) are still in existence. Addition of a slight excess of electrolyte of opposite charge causes immediate precipitation.

*Lyophilic*<sup>3</sup> sols have a much greater degree of stability than lyophobic owing to interaction between their two phases. They cannot be broken either by centrifuging or by addition of electrolyte. Even when electrically neutral they still retain a large part of their stability. Lyophilic sols with water as the dispersion medium can only be coagulated by addition of strong dehydrating agents such as alcohol or saturated salt solutions. In a mixture of gold (lyophobic) and gelatine (lyophilic) sols the gelatine coats the gold particles and so gives the whole system stability.

The biologically important colloids are mostly lyophilic as are the many industrial colloidal materials, lacquers, textiles, soaps, adhesives, explosives and so on derived from them. Proteins, the most important of all biological colloids, form stable sols with water,

<sup>1</sup> Greek λύω (luō), dissolve; and φοβέω (phobeō), cause to flee.

<sup>2</sup> R. Brown, botanist, studying *Lycopodium* spores in 1826.

<sup>3</sup> Greek φιλος (philos), loving.

34 SOME PHYSICAL CHARACTERS OF ORGANIC SUBSTANCES  
but they are fairly easily dehydrated. They carry electrical charges of both positive and negative sign which are easily influenced by external conditions. When these are equalised and reduced to a minimum the protein may coagulate. Protein sols are therefore in some respects intermediate between the lyophilic and lyophobic categories.

### *Microscopic, Ultramicroscopic and Submicroscopic Particles*

The larger colloidal particles, as in Indian ink, are just big enough to be seen under the high power of the microscope. When they are freely suspended and not attached to the slide or coverslip they appear in a continual jerky Brownian movement. The disperse particles of finer sols such as gold or Congo Red are too small to be seen even under the highest magnifications of the microscope and the sol appears clear. The limit of microscopic vision lies at about  $150\text{ m}\mu$  but the presence of still smaller particles can be detected by viewing the sol against a dark background with a beam of light passing through from the side. As seen by the naked eye the sol then appears milky (Tyndall effect), but a true solution remains optically empty. When viewed through a microscope the milkiness is resolved into discrete dots of bright light that reveal the presence—but not the shape—of the ultramicroscopic particles. The dots are in Brownian movement which is more pronounced than that seen by direct illumination because the particles concerned are smaller. In a cell under dark-ground illumination the vacuole appears dark and empty (solutes in true solution) but the colloidal wall and protoplasm are brilliantly lit.

The shape of ultramicroscopic and colloidal particles can be revealed by the electron microscope which has recently been applied to such studies. Biological materials unfortunately do not present much contrast to penetration by electrons and so are less readily investigated than the mineral colloids, but much has already been done. The table on p. 35 gives the range of magnitudes of the smaller objects dealt with in this book.

### *Internal Surface of Colloids*

The very large number of particles or droplets forming the disperse phase of a colloid sol present collectively an enormous surface. If we take a solid spherical object such as an orange and cut it into halves it is clear that we have greatly increased the exposed surface, for to the original external surface we have added the cut surface of the two halves. If we now cut the halves into quarters the total sur-

TABLE OF MAGNITUDES

	Approximate diameter
<b>MICROSCOPIC PARTICLES</b>	
<i>Volvox aureus</i> (p. 108) . . . . .	200–500 $\mu$
<i>Pleodorina</i> (p. 106) . . . . .	170 $\mu$
<i>Amœba proteus</i> (p. 17) . . . . .	100–250 $\mu$
Limit of direct vision . . . . .	100 $\mu$
<i>Eudorina</i> (p. 105) . . . . .	40–150 $\mu$
<i>Euglena</i> (p. 22) . . . . .	50 $\mu$
<i>Pandorina</i> (p. 103) . . . . .	20–40 $\mu$
<i>Protococcus</i> (p. 21), <i>Chlamydomonas</i> (p. 97) . . . . .	10–20 $\mu$
Yeast (p. 340) . . . . .	10 $\mu$
Clay suspension particles . . . . .	3 $\mu$
Coccus (spherical bacterium) . . . . .	1 $\mu$
Limit of microscopic vision . . . . .	$\Delta$ 0.15–0.2 $\mu$
<b>ULTRAMICROSCOPIC PARTICLES</b>	
Viruses . . . . .	20–200 $m\mu$
Bacteriophages . . . . .	8–30 $m\mu$
Gold sol particles . . . . .	2–15 $m\mu$
Limit of ultramicroscopic detection . . . . .	5 $m\mu$
Limit of electron-microscopic detection . . . . .	3–5 $m\mu$
<b>SUBMICROSCOPIC PARTICLES</b>	
Large molecule—soluble starch . . . . .	50 $\text{\AA}$
Medium molecule—glucose . . . . .	6 $\text{\AA}$
Smallest molecule—hydrogen . . . . .	1 $\text{\AA}$
$\mu$ (micron) = mm/1,000; $m\mu$ (millimicron) = $\mu$ /1,000; $\text{\AA}$ (Ångstrom unit) = $m\mu$ /10.	

face is still further increased and the more we divide the orange the greater is the surface exposed. The surface of a cube having 1 cm. edges measures 6 sq. cm. and its capacity is 1 cc. Its *specific surface*, i.e. its surface per cc. of volume is therefore 6 sq. cm. If the cube were subdivided into smaller cubes with 10  $m\mu$  edges, i.e. colloidal dimensions, the specific surface would rise to  $6 \times 10^{15}$  sq. cm. Thus the collective surfaces of all the disperse particles in a drop of colloidal sol are immensely greater than the surface that would remain if all the particles were aggregated in a single mass. This has remarkable consequences.

### Surface Energy and Adsorption

Where solid or liquid matter is in contact with matter of another kind, the surface between them is the seat of free energy because of the break in the action of molecular forces. This becomes apparent in what is called surface tension (Fig. 19). The surface of a drop of liquid in air, for instance, tends to shrink until the drop becomes a sphere, the figure with the smallest possible area in relation to the

mass of the liquid, and therefore with the minimum free energy. Liquids with a high surface tension form drops which do not easily spread upon a solid surface. Mercury, water and alcohol form a series of liquids with decreasing surface tension, and an increasing readiness to "wet," i.e. spread upon, a clean sheet of glass or similar surface.

The enormous collective surface, i.e. the sum of all the surfaces, of the disperse particles or droplets of a sol, involves a corresponding amount of surface energy of the particles or droplets. This is of very great importance in determining the behaviour of the colloid towards liquids, solutes and other sols which may be attracted to the surfaces of the disperse particles or droplets and held there by the surface energy, at the same time decreasing the surface tension of the dis-

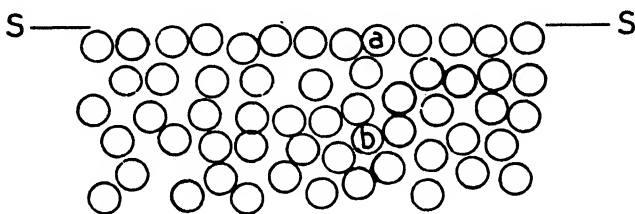


FIG. 19.—Diagram to illustrate the nature of surface tension. Each circle represents a molecule of the liquid; S—S the liquid surface. A molecule such as *b* is attracted by neighbouring molecules more or less equally in all directions; but a molecule in the surface, such as *a*, tends to be dragged into the body of the liquid on account of the attractions on that side, unbalanced by any upward attractions. As a result, the whole surface tends to shrink to the least possible area.

perse phase. This process is called adsorption. The living protoplasm of the cell is believed to be a colloidal sol of which the continuous phase is a solution of various crystalloids and the disperse phase consists mainly of protein and fat droplets or particles. These take up and hold by adsorption molecules and ions of solutes which diffuse into the cell and come within the range of their surface energy. In this way large quantities of various substances may be taken in and held in the living cell. Dyes are taken up in the same way by protoplasm and by the other organic colloids of the plant or animal, and on this process largely depends the staining of tissues employed in making microscopic preparations and also the dying of textile fabrics.

### Gels

Both lyophobic and lyophilic sols can flow freely, though the latter may also become viscous. There is also a class of colloidal

systems having a large measure of rigidity and resisting forces tending to make them flow. These are the gels. The disperse phases of the commonest biological gels have long thread-like molecules sometimes with side branches. When one of their hydrosols (sols with water as the continuous phase) loses water the disperse particles get closer and closer together and finally become entangled so that the sol becomes viscous and resistant to flow and eventually shows an elasticity resembling that of rubber. If the molecular chains besides becoming entangled, also tend to interact and become laterally attached, then a more rigid and less elastic gel results. Protein gels appear to be of this type. Gelatine, (a protein extract of hide and bones) dissolved in water forms a viscous sol which sets on cooling into a rigid gel. This may be changed back to a sol by

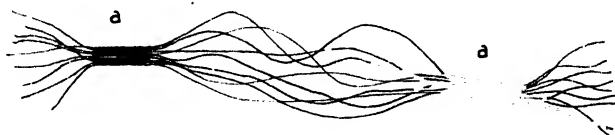


FIG. 20.—Diagram to illustrate the nature of a gelatine gel. Each line represents a thread-like protein molecule; *a*, *a* points of adhesion of molecules which are free at other parts of their length.

heating to a few degrees above the gelation temperature or, more slowly, by adding more water. The sudden change of rigidity at gelation is explained by supposing that the long thread-like gelatin molecules form adhesions at certain points along their length, so building up colloidal particles or *micelles* which are linked together in the gel by the free solvated parts of the chains (Fig. 20). Much water is still present in the parts between the micelles and if this is withdrawn by adding alcohol the gel structure is destroyed and gelatine precipitated out. Less drastic withdrawal of water causes the gel to shrink and become more solid. In this condition it becomes a powerful absorbent for water which it “imbibes,” gradually swelling and passing back into a sol. The forces involved in *imbibition* are very powerful, especially if a little acid or neutral salt is also dissolved in the water. The gels in dry seeds, spores and seaweed mucilages take up water with immense power. Grain ships carrying wheat in bulk are known to have been sunk owing to the penetration of sea water through small leaks causing the wheat to swell and burst open the hull.



*Diffusion and Dialysis*

A very important difference between crystalloids and colloids, a difference used by Thomas Graham (who first investigated the subject in the middle of last century) to distinguish between them, is their relative *diffusability*.

If a strong (concentrated) solution of a crystalloid is brought into contact with a weak (dilute) solution of the same crystalloid in the same solvent, diffusion proceeds until the solute is equally distributed through the whole of the liquid. *This is an expression of the general physical law that all systems tend towards equilibrium.* The rate of diffusion varies directly with the difference in concentration of the two solutes and with the temperature, inversely with the diameter of the molecule of the solute. If now the two solutions of different concentrations are separated by a thin membrane, such as vegetable parchment, crystalloid solutes will diffuse through the membrane as they would diffuse into a liquid with which they were directly in contact, though less rapidly. The rate of this diffusion through a membrane depends partly on the nature of the membrane and partly on the size of the molecule of the solute, partly again on the chemical and electrical relations between the solute and the membrane.

The disperse phase of a colloidal sol, on the other hand, does not in general pass through a membrane at all, or only does so with extreme slowness, and this again depends on the size of the particles, on the nature of the membrane and on the chemical relations between them. It was this difference which Graham used to distinguish colloids from crystalloids, and he showed that a colloid and a crystalloid in mixed solution could be separated by placing the solution in a parchment bag and plunging the bag into water, when the whole of the crystalloid would eventually escape through the membrane leaving the colloid pure behind. This process is called *dialysis*.

We may say broadly that *crystalloids in solution will dialyse and that colloids will not*. But different crystalloid solutes pass through a given membrane at very different rates. Sucrose (cane sugar) with a molecular size just below the colloid range, behaves as a crystalloid, but passes a parchment membrane with extreme slowness. The membrane may be likened to a sieve with meshes of definite size though varying within limits. These meshes will let through molecules up to that size, but not larger ones. The disperse particles of a colloid sol are in general too large to pass through the membrane

but in some cases they may be just little enough to pass in small numbers. The matter is further complicated, as we have seen, by the possibility of reaction between the molecules of the solute or disperse phase and those of the membrane. Some substances appear to owe their ability to pass through a membrane to their solubility in its substance.

## Practical Work

### A. CRYSTALLOIDS AND COLLOIDS

(1) Place some crystals of potassium bichromate at the bottom of a test tube, and add about 5 ml. water and warm. Note that the crystals rapidly disappear to give a clear coloured solution. Examine a drop of the solution under the microscope—it is clear. If dark-ground illumination is available, use it to examine the solution also—it will still be clear. Pour a little of the solution on to a watch glass and allow it to evaporate. Fine crystals will be reformed. Potassium bichromate is a typical crystalloid.

(2) Dissolve a little Congo Red in a test tube as above. If necessary filter. A clear red solution is obtained. Examine under the microscope; it is still clear, but with dark-ground illumination it appears cloudy with bright points of light under the microscope. Congo Red is a fine suspensoid sol with particles of ultra-microscopic size.

(3) Put one drop of Indian ink in a test tube and dilute with water until you can see through the mixture. Examine a drop under the high power of the microscope. Numerous small solid particles are visible. They are in Brownian movement. Note that the smaller the particle the more pronounced is the movement. Do not be misled by particles that have become attached to the slide or coverslip. The Brownian movement of the free particles continues indefinitely. Indian ink is a coarse suspensoid and lyophobic sol with particles up to microscopic dimensions.

(4) Put a little powdered gelatine or glue or agar<sup>1</sup> into a test tube. Add 5 ml. of water and warm. An opalescent sol is obtained. Allow to cool. It will set to a gel. Warm again gently, preferably in a bath of hot water. It will return to the sol condition. Pour on to a watch-glass. When cool, note that the gel retains its shape (cf. table jellies, which consist principally of gelatine turned out of a mould).

(5) Place a rectangular strip of dry gelatine on a sheet of glass over squared paper. Mark the edges of the gelatine with Indian ink opposite the divisions of the paper. Allow the ink to dry, then dip the gelatine in water and float it on the glass in a little water. Note the gradual expansion of the gelatine as it absorbs water. After a time measure the increase in area of the gelatine strip by again placing the glass over squared paper. Now transfer the gelatine to a piece of fine muslin and hang it up to dry. It contracts and gradually decreases in area owing to loss of water. The gelatine is a colloid gel.

(6) Put 25 ml. of water into a 50 ml. measuring cylinder. Add 10 dry peas and measure their volume by the rise of the water. Allow them to soak in a dish for at least twenty-four hours and then measure their volume as before. By what percentage has the imbibed water increased it? The hydration of the colloidal material in the dry seeds is a necessary preliminary to germination.

<sup>1</sup> Agar is dried mucilage from various species of red seaweeds.

## B. DIFFUSION OF CRYSTALLOIDS AND COLLOIDS. DIALYSIS

(7) Add a little potassium bichromate solution to a warm gelatine sol and pour 1 or 2 ml. into a warm test tube. Allow to set. Prepare a tube similarly with a gel impregnated with Congo Red. Clamp the two test tubes firmly, to avoid shaking, in front of a white background and half fill each tube with water. The potassium bichromate will diffuse into the water quickly, but the Congo Red much more slowly.

(8) Mix about half a gram of soluble starch with cold water and pour it into 100 ml. of boiling water in a beaker. Filter while hot and dissolve about half a gram of common salt in it. Pour the mixture into a parchment paper thimble and hang the thimble in a beaker of distilled water, which gives no reaction with silver nitrate. After one hour test samples of the distilled water for chloride (salt) with silver nitrate, and for starch by adding iodine solution.

## Chapter IV

# PROTOPLASM AND THE CELL

### Protoplasm

The simple organisms *Amæba*, *Protococcus* and *Euglena*, described in Chapter II, illustrate some of the characteristics of protoplasm in three of its diverse manifestations. To begin with, they all have great similarities. They are all minute (10–100  $m\mu$  diameter) and with the rarest exceptions protoplasm is always organised into cells of similar sizes. It is usually in the physical state of a colloidal sol; but forms gel membranes at its surfaces. This happens even in *Protococcus* though it is not so easy to appreciate as in *Amæba* and *Euglena*. A gel membrane can, however, be readily detected round the egg cells of the seaweed *Fucus*, which are without cell walls. Gel membranes are not restricted to animal cells alone. A fluctuation from sol to gel condition must be going on continuously in active *Amæbae* and, in cells generally, such changes are usually produced by change of acidity or by enzyme action.

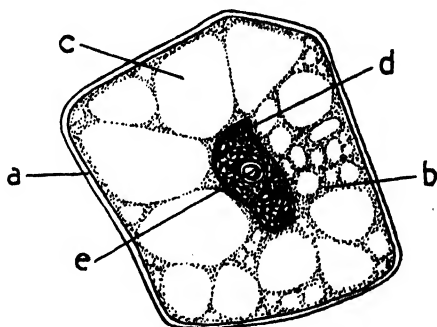


FIG. 21.—Diagram of a plant cell. *a*, cellulose wall; *b*, cytoplasm; *c*, vacuole; *d*, nucleus; *e*, nucleolus.  $\times$  about 400.

Protoplasm, as seen under the microscope, is always granular and always includes a nucleus (Fig. 21 *d*). The other inclusions vary in size from the relatively large chloroplasts of *Protococcus* (Fig. 12) downwards. Some, which are on the limits of microscopic visibility, are called *mitochondria*. They can be made visible by treatment with certain mitochondrial stains such as Janus Green. They have also been detected with the ultramicroscope. Their status has been much

debated; some investigators regard them as constant cell organs comparable with the chloroplasts and other plastids and being perhaps their forerunners: others regard them as metabolites, probably of a fat-like nature. Examination of cells in the ultramicroscope (dark-ground illumination) reveals even smaller particles which are often in Brownian movement. This shows that the protoplasm is colloidal and, partly at least, in the condition of a sol. Other colloidal properties shown by protoplasm are its inactivation at temperatures about 50° C. due to heat coagulation; its "fixation" by coagulating agents such as trichloroacetic acid and iodine; its reversible changes from sol to gel in an electric field as shown by the temporary cessation of Brownian movement; and its shrinkage during drying, and swelling when wetted. Associated with this last is its loss of activity when dry (cf. *Protococcus*, p. 21) and its recovery when wetted again.

The colloidal nature of protoplasm results from the great size of the protein molecules of which it is largely composed. It is not, however, a simple protein colloid, such as gelatine or egg albumin. Its continuous phase holds numerous sugars, plant acids, salts and other soluble substances in true solution, and the dispersed particles previously mentioned are of many chemical sorts, polysaccharides, fatty substances and many others as well as proteins. The constitution and structure of the disperse phase is, further, markedly affected by the solutes of the continuous phase, such as salts of calcium and magnesium. On the immense internal surface of the protein particles many spots are catalytic (see enzymes, p. 81) and are able to promote changes in the freely moving substances dissolved in the continuous phase.

### *Cells and the Cell Doctrine*

With relatively rare exceptions, living matter is organised into cells. The whole body of an *Amæba* or *Protococcus* consists of a single cell; but cells are unable to grow beyond a certain very limited size and unicellular organisms are all microscopic. Each cell nucleus tends to gather, or grow, round itself a certain definite amount of cytoplasm. When this is exceeded the cell and the nucleus itself may divide. All large organisms, plant or animal, are multicellular, that is, built up of numerous cells and their products. A large plant does not have larger but more numerous cells than a small one. The cells average the same size in the leaves of an ordinary water-lily, in the giant *Victoria regia* and in the ten-foot long leaves of the Japanese *Euryale ferox*.

Every multicellular organism begins life as a single cell. Development consists of the division, growth, cohesion and differentiation of this original germ cell and its progeny. The daughter cells do not separate, like the daughter cells of *Amæba* and *Euglena*, but remain more or less firmly attached to one another, so building up a cell mass. A faint foreshadowing of this condition is seen in the cell aggregates of *Protococcus* (p. 22). As growth goes on the cells develop different characteristics to give rise to the different tissues and organs of the adult body. The generalisation that all organisms consist of cells and products of their activity is known as the *cell doctrine*. It is not, however, strictly true to say that the properties and functions of the organisms as a whole are the sum of those of its constituent cells. Some of its attributes, for example, exist only as a result of their co-ordination.

Some exceptions to the cell doctrine must be admitted. Among the lower forms of life some have not developed a cellular structure though they may show definite structure and differentiation of other kinds. The Myxomycetes, or slime fungi, have a body consisting of a thin sheet of naked protoplasm spreading irregularly over an area as big as one's hand (Fig. 18 D). It has no divisions into cells though it has many nuclei; it resembles to some extent a sheet consisting of thousands of *Amæbae* run together without their gel membranes.

In some of the algæ and fungi the plant body is composed of tubular walls enclosing a continuous mass of cytoplasm containing many small nuclei. The tubes may be branched and have occasional cross walls. The protoplasm at the tips of the branches increases as the plant grows and the nuclei multiply by repeated divisions. The wall continuously has new substance added to it from the active protoplasm within, and is pushed out ahead as the tube grows in length. Here there is no cell structure and such plants are called *non-cellular* or *cænocytic*<sup>1</sup> (see, for example, *Mucor*, p. 363). *Valonia*, a green alga, builds up spheres of 1-4 cm. diameter. The centre is occupied by a large vacuole containing up to 50 ml. sap round which the protoplasm forms a thin cænocytic layer.

Animal cells are frequently less clearly marked off from one another than plant cells, since they do not secrete cellulose walls over their surfaces. Sometimes a network of cytoplasm is developed with a nucleus at each node of the mesh where the branches meet. The integration of animal cells into tissues has gone much further

<sup>1</sup> Greek *κοινός* (koinos), common and *κύτος* (kutos), a hollow vessel.

than the integration of plant cells and there is necessarily a corresponding loss of independent cell structure.

A set of similar cells which are built into a unit and perform a common function is called a tissue.<sup>1</sup> In highly organised plants there are absorbing, conducting, insulating and other tissues; in animals the heart, lungs, liver and so on are built of closely integrated cells and each has its own function to perform for the organism. Every cell within a tissue must be able to carry on the principal vital functions such as assimilation and respiration or it would fail to live; but in company with its neighbours within the tissue it specialises in one function of protoplasm which they carry out on behalf of the organism as a whole. The fibres of muscle tissue (Fig. 22 F) have the power of contracting, a specialised form of protoplasmic movement, developed to a very high degree. By means of their co-ordinated contractions the animal moves. There are groups of cells in most flowers which have developed an altogether abnormal capacity for secreting sugar solutions. Collectively they form the nectaries, secreting tissues which, on behalf of the whole plant, provide the means of attracting insects for pollination.

The cell is recognised primarily as a unit of plant or animal structure. It has been said that the cell doctrine has done as much for the study of plants as the atomic theory has done for chemistry. There must, however, be one very important reservation: however convenient a unit the cell may be in the study of structure, it has never had the same usefulness in the study of function. The existence of tissues and the fibrils of protoplasm uniting one cell with the next (Fig. 1) are two obvious reasons, and in biology the unit, whether cell, tissue, organism or population must be chosen according to the particular problem in mind.

### *Cell Walls, Intercellular Substance and Intercellular Spaces*

The whole substance of a mature plant or animal body does not consist only of cells, but also includes matrices of non-living matter in which the cells are confined or embedded. All such substances have been produced by the activities of the living protoplasm. In animals the secretions from neighbouring cells frequently run together so that a more or less uniform *intercellular substance* is formed. This is clearly seen in cartilage (Fig. 22 C). In areolar connective tissue the intercellular substance is differentiated into fibres of two different

<sup>1</sup> Latin *texere*, to weave, via French, *tissu*, woven, referring to the analogy of its appearance with a textile fabric.

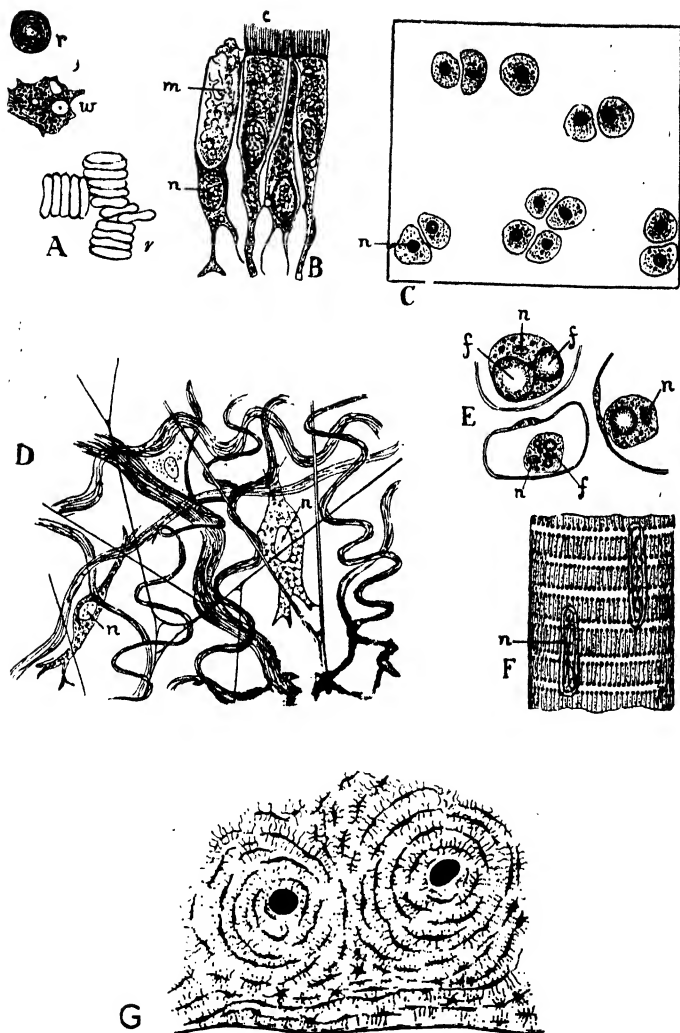


FIG. 22.—Cells from different tissues of a vertebrate animal. A, blood corpuscles; *r*, red corpuscles, cells without nuclei; *w*, white corpuscles with appearance and movements similar to *Amœba*. B, glandular epithelium lining trachea leading to lungs; *n*, nucleus; *m*, mucus expelled from a mucus cell; *c*, cilia. C, cartilage cells embedded in cartilaginous matrix secreted by the cells; *n*, nucleus. D, connective tissue; *n*, nucleus. The stripes are fibres developed in the intercellular substance. E, fat-forming cells; *f*, fat globules; *n*, nucleus. F, striped muscle fibre consisting of many fused cells; *n*, nucleus. G, bone; the small dark slits are lacunæ in which the cells formerly existed, separated by concentric rings of calcified intercellular matrix.



kinds, in addition to the simple ground substance (Fig. 22 D). These fibres differ altogether from the fibres of muscle which are formed of the protoplasm itself.

Plants very rarely have intercellular substance; but a notable exception is afforded by *Fucus* (p. 128) in which the central cells are embedded in a matrix of mucilage of their own production. It is one of the special characteristics of plant cells that they secrete firm cellulose walls round them. The cell walls in the aggregate form the skeleton of the plant, and a great part of the higher plants, and especially of those that are trees, is composed of hardened and thickened cell walls. There are obviously great similarities between cell walls and intercellular substance, particularly when the latter is hardened by mineral deposits, as in bone (Fig. 22 G). Cell walls are always composed of carbohydrates, however, and, strictly speaking, are laid down not outside the cell surface but just inside the original *middle lamella*. They are usually penetrated by fine threads of the protoplasm itself (Fig. 1).

Another feature of the tissues of the higher land plants is the existence of a system of *intercellular spaces*. During the laying-down of the thickening cellulose layers of the wall, the cell surface becomes strongly elastic and the cells tend to round themselves off as much as possible. As a result they come away from one another, especially at the corners, and a system of more or less continuous air passages is developed. This occurs to its fullest extent in the mesophyll of leaves and is illustrated in Fig. 143, p. 226. A channel by which gases such as oxygen may enter from outside, and water, vapour and carbon dioxide produced by the cells may leave the tissues is thus set up. It is of great consequence in bulky plants, none of which possess active organs of breathing comparable to gills and lungs.

### *The Plant Cell—Parenchyma*

The first cells to be described were the dead cells of a piece of cork. They were seen by Robert Hooke in 1667 with the compound microscope that had been devised a few years earlier. He compared these cork cells with those of a honeycomb and first gave them the name. It was thus to dead walls enclosing empty cavities that it was first applied. It was not until 1831 that Robert Brown discovered the nucleus and a few years later that von Mohl realised the significance of the semi-transparent lining to the walls and named it protoplasm.<sup>1</sup>

<sup>1</sup> Greek *πρωτος* (*prōtos*), first and *πλασμα* (*plasma*), thing formed or moulded as from clay or wax.

The name was afterwards extended to the similar living material of animals and the term *cell* gradually came to be used in its modern sense of a living unit which may or may not have cell walls. The name

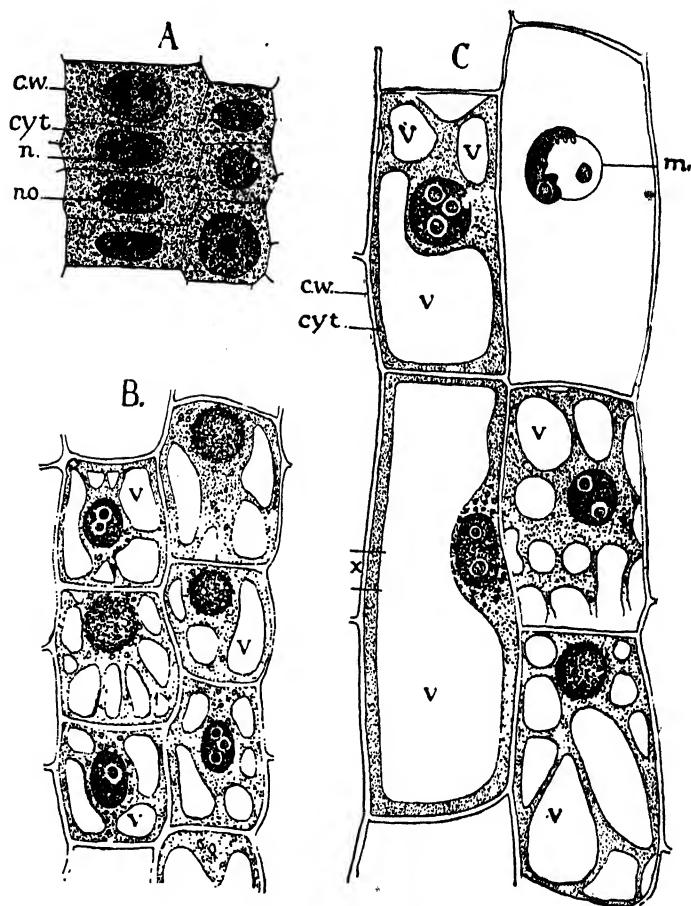


FIG. 23.—A, embryonic cells from the meristem (growing point) of the root. B, beginning of vacuolation. C, vacuolation completing itself. cw, cell wall; cyt, cytoplasm; n, nucleus; no, nucleolus; v, vacuole; m, a cell that has been cut open: most of the contents have escaped but the broken nucleus is forming a new membrane in contact with water.  $\times 660$ . After Sachs.

is also still applied to those dead walls surrounding empty cavities after the protoplasm has perished, which form such important parts of the skeleton (wood) and coverings (cork) of plants.

The adult plant cell is usually also characterised by the possession

of a large central *vacuole*.<sup>1</sup> This is a space filled with a watery cell sap enclosed within the cytoplasm (Fig. 23 C). This often becomes so large a part of the whole cell that the protoplasm is merely a thin layer lining the wall. The nucleus is always embedded in the cytoplasm and bulges the thin layer out into the vacuole or more rarely remains suspended in the centre of the cell in cytoplasmic bridges (Fig. 21). The term *vacuole* was given under the impression that it was really as empty as it appears; but it is actually a solution of numerous substances of great importance to the life of the cell. A cell of the kind just described, characterised by a plain cellulose wall and large central vacuole, is called *parenchymatous*, and a tissue of such cells a *parenchyma*.<sup>2</sup> They provide the ground tissue filling in between more highly specialised types and represent the adult plant cell in its most generalised form.

### *Meristematic Cells*

In the higher plants new cells are produced mainly by division of pre-existing cells at or near the tips of branches of roots and shoots. The regions of active cell division are called *meristems*.<sup>3</sup> These cells are all young because they are repeatedly dividing so long as active growth continues. The characteristic features of meristematic cells are thin cell walls—the thickening layers of cellulose being a later development—and a cell cavity completely filled with protoplasm including a conspicuous central nucleus (Fig. 23 A). In these cells the nucleus frequently has a diameter up to three-quarters of that of the cell. The granular *endoplasm*<sup>4</sup> contains granules and droplets of various sizes which are probably plastic substances consumed in cell growth. It also contains small plastids and mitochondria (p. 41). The boundary layer of *ectoplasm*<sup>5</sup> is only just visible under the microscope, being only a fraction of a micron in thickness.

### *The Nucleus*<sup>6</sup>

The nucleus is an almost invariable feature of living cells; the only exceptions being the highly specialised sieve-tubes (p. 200) of higher plants and the red blood corpuscles (Fig. 22 A) of animals. It is in many ways the most remarkable of all parts of the cell. Its importance to the life of the cell can be inferred from its behaviour and from

<sup>1</sup> Diminutive from Latin *vacuum*, an empty space.

<sup>2</sup> Greek *παρεγχυμα* (*paregkhuma*), something poured in beside; referring to its filling in between more specialised tissues.

<sup>3</sup> Greek *μεριστής* (*meristēs*), divider.

<sup>4</sup> Greek *ἐνδον* (*endon*), within.

<sup>5</sup> Greek *ἐκτός* (*ektos*), outside.

<sup>6</sup> Latin, kernel.

the behaviour of cytoplasm deprived of its nucleus. Some of the larger *protozoa*<sup>1</sup>—unicellular animals—have been deprived of their nuclei by means of a micro-pipette. Of fifty individuals so treated none lived more than five days. Removal of small parts of the cytoplasm had no such destructive effect, and if the nucleus was returned shortly after its removal the organism was able to live and give rise to thriving colonies. The protoplasm of some plant cells divides when it is caused to shrink away from the walls by severe plasmolysis (p. 60). It has been shown that only those fragments in organic contact with a nucleus are able to survive and form new cell walls (Fig. 24 A). The parts without the nucleus remain alive for a time, but they apparently cannot assimilate and soon die. In particularly active cells, such as those of meristems, the nucleus is always large and conspicuous. Again, when local activity is going on within a cell, the nucleus commonly moves to the spot in which work is being carried out (see Fig. 24 B). This is readily seen in pollen grains (Fig. 99, p. 174) and root hairs (Fig. 157, p. 248), cells which form long tubular outgrowths. The nucleus is always found near the tip of the tube where new wall material is being laid down. Similarly, whenever special wall thickenings are being developed, the nucleus migrates to the spot (Fig. 24 C and D). Facts like these suggest that the nucleus exercises an essential influence over the metabolic and formative cell processes; but exactly how it does so is still a mystery.

The nucleus contains the principal hereditary materials that are handed down from parent to offspring and that are the cause of their resemblances. This is so important that the structure and behaviour of the nucleus have been more intensively studied than those of any other part of the cell.

The nucleus is separated from the protoplasm by a special *nuclear membrane* which may be tough enough to be pulled off with a micro-needle. It is probably a protein gel. The contents of the nucleus form a watery sol in which one or more *nucleoli* may be visible. They usually occupy about one twenty-fifth of the nuclear volume and are dense enough to be driven out into the cytoplasm by centrifuging. Their significance is obscure and they have been regarded as food reserves or as pieces of cytoplasm included within the nucleus. More important are the *chromosomes*.<sup>2</sup> These are long, narrow threads. At the time of nuclear division they take up the stains which react with nucleic acid (p. 81) much more freely than the other compo-

<sup>1</sup> Greek *πρωτος* (prōtos), first; *ζων* (zōn), animal.

<sup>2</sup> Greek *χρωμα* (chrōma), colour and *σωμα* (sōma), body.

nents of the nucleus. This is the colouring referred to in their name. Normally they are colourless like the rest of the protoplasm. During the metabolic stage, sometimes still called the resting stage of the

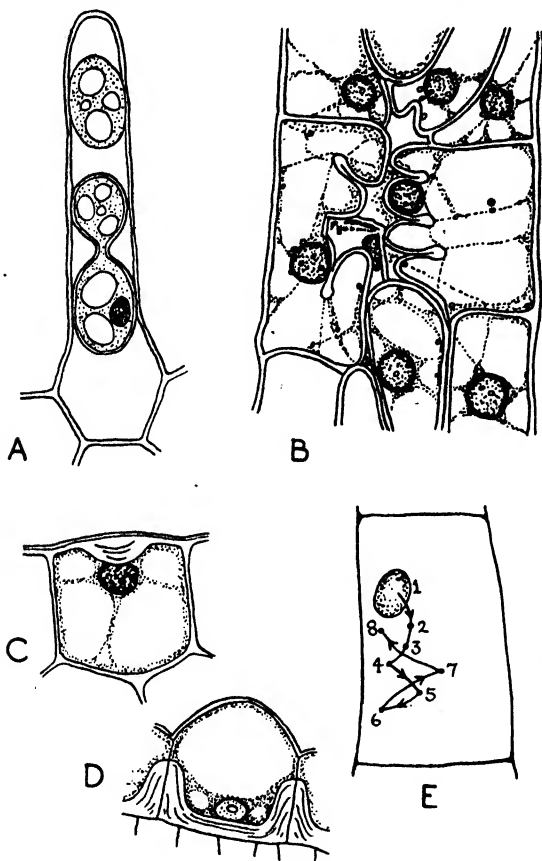


FIG. 24.—A, hair of *Cucurbita pepo* strongly plasmolysed. The protoplasm has divided into two fragments. The lower half containing the nucleus has formed a new cell wall.  $\times 320$ . After Pfeffer. B, epidermal cells of *Tradescantia virginica* forming new walls. Note the position of the nuclei where active regeneration is going on.  $\times 200$ . After Miehe. C, epidermal cell of *Aloe verrucosa*, and D, epidermal cell of *Scopolina atropoides*, both with nuclei at the point of wall thickening. After Haberlandt. E, migration of the nucleus in a hair-cell of *Bryonia dioica*.  $\times 200$ . After Zimmermann.

nucleus, they are much drawn out and intertwine freely. They probably do not form cross-connections to build a mesh, as was formerly supposed. They are comparatively fluid and may practically fill the whole volume of the nucleus, though in some nuclei a

nuclear sap is also present. Detailed observation of the chromosomes at this stage is difficult because they do not stain readily and knowledge of their finer structure depends mostly on observations at the time of nuclear division.

### *Mitosis*<sup>1</sup>

The essential feature of nuclear division is the sharing out of the chromatic material between the two daughter nuclei. In the almost invariable method of doing this, which is called mitosis, *the identical halves of split chromosomes are separated into two identical groups* from which the daughter nuclei are developed. In all its main features this process is identical in plants and animals, both simple and complex; the differences met with are only of minor importance. The ordinary methods of examination always permanently stain and coagulate the proteins and so kill the cell and "fix" it at a particular stage. Neighbouring cells in a meristem may exhibit different stages at the moment of fixation. In a few types of nuclei, particularly favourable for observation, successive stages have been watched step by step in the living material. Recently, with the help of a new optical device, the phase-contrast microscope, it has become possible to film the phases of mitosis and watch their progress on the screen. Four successive stages may be recognised for convenience of description.

*Prophase.*<sup>2</sup> The onset of nuclear division is first indicated by the appearance of coiled and contorted threads which are more or less evenly spread throughout the whole body of the nucleus (Figs. 25 and 26). An important point is that, as soon as the threadlike chromosomes are clearly visible, they are seen to be divided longitudinally except at a single point where they remain single. Although separate, they do not fall apart at the ends but remain together throughout their lengths. Each half chromosome is called a *chromatid* and the point where they remain single is called the *centromere*.<sup>3</sup> The chromosomes are markedly constricted at the centromere which differs in its position along the thread in different chromosomes but is rarely, if ever, found right at the end. It stains much less than the rest of the chromosomes and may therefore look almost like a break in the thread. The threads now contract and may shorten to about a tenth of their length when first distinguishable. Their loss of volume

<sup>1</sup> Greek *μῖτος* (mitos), thread, referring to the threadlike structures appearing in the process.

<sup>2</sup> Greek *πρὸ* (pro), before.

<sup>3</sup> Greek *κέντρον* (kentron), the point or centre; *μέρος* (meros), part. Here centre of importance not structure.

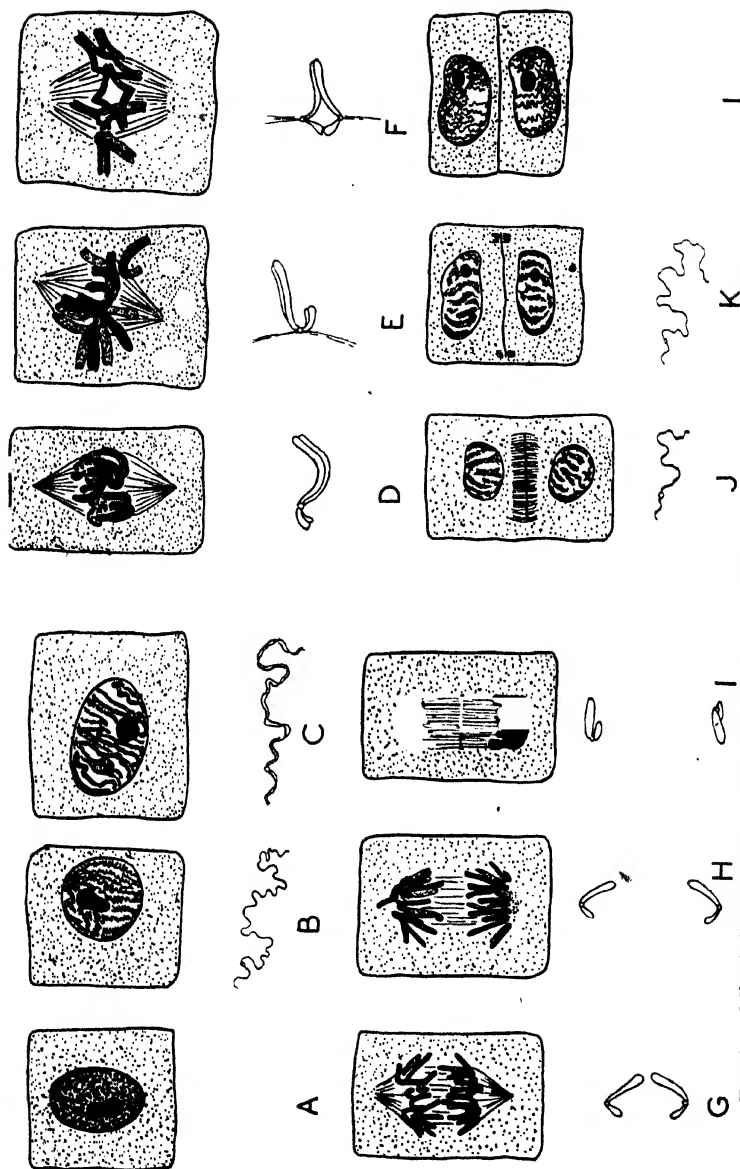


FIG. 25.—Mitosis in meristematic cells of the root tip of *Allium cepa* (onion). A–C, prophase. D–E, metaphase. F–H, anaphase. I–L, telophase. After Buchner. The condition of a single chromosome is shown below each nuclear stage.

is much less, so they simultaneously become much thicker and take on the appearance of rods rather than threads. This appears to be the result of a partial loss of water and the nuclear contents are now more sharply divided into chromosomes and watery sap. The original form of the chromosomes was probably a loose spiral and the dehydration of their colloids causes the coils to tighten up until they are closely packed. It is presumed that the rods are in reality such closely packed spirals, though this only becomes clearly visible when they begin to loosen again at a later stage (telophase). When contraction is complete, the form of the rods is interrupted by one or more constrictions in addition to the centromere, which have definite positions and give to different chromosomes characteristic shapes by which they can be recognised in successive nuclear divisions (Fig. 28). As prophase progresses the nucleoli and the nuclear membrane disintegrate and disappear.

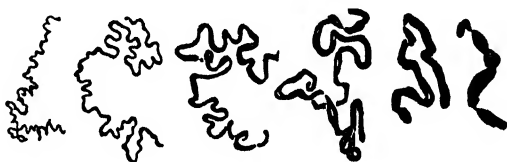


FIG. 26.—Contraction and uncoiling of the spiral in chromosomes of *Fritillaria* during prophase.  $\times 1200$ . After Darlington.

*Metaphase.*<sup>1</sup> When the chromosomes have reached their full contraction a new element enters the process. This is the *spindle*, which has a typical spindle shape and lies across the nucleus, usually in the long axis of the cell, with its tips or poles projecting into the cytoplasm, the nuclear membrane having disappeared. In the cells of animals and of some primitive plants the spindle is associated with a body called the *centrosome* (Fig. 27 A) which divides into two *asters*. The asters travel to opposite sides of the nucleus and the spindle forms between them. In the cells of the higher plants no centrosomes or asters are visible, but the spindle forms across the nucleus and obliterates its outline in much the same way. When the spindle is dehydrated by fixing agents it contracts laterally and may show lines of longitudinal shading. This and other observations suggest that the spindle possesses some kind of longitudinal structure, possibly because the long chains of its protein molecules are arranged in that direction. Up to this point the chromosomes have remained

<sup>1</sup> Greek *μετά* (meta), after.



more or less evenly distributed throughout the nucleus; but now they move into a definite position midway between the two poles of the spindle. Here they form an equatorial plate at right angles to the spindle's long axis. Each chromosome is associated with the

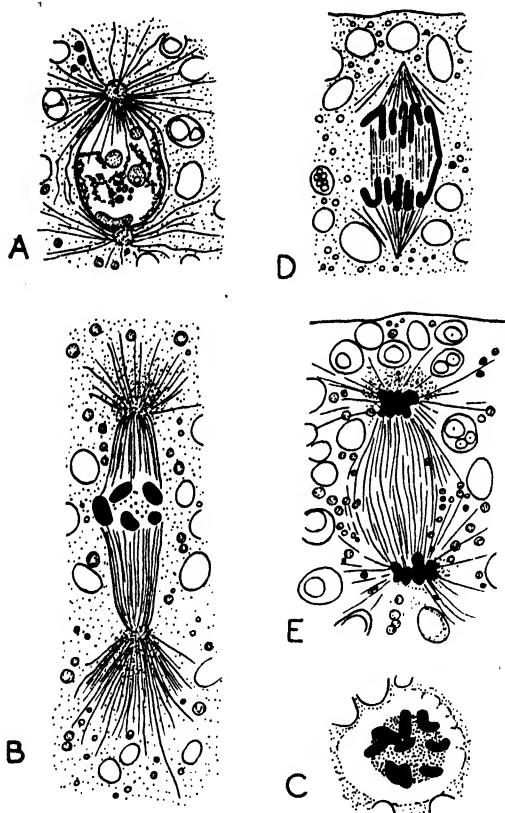


FIG. 27.—Mitosis in *Pellia*, a liverwort. A, prophase showing two asters at top and bottom of the nucleus. B, late prophase with spindle; radiations visible at poles but not the asters themselves. C, transverse section showing "metaphase plate". D, anaphase, radiations and asters not visible. E, telophase, radiations have reappeared but not asters.  $\times$  about 1000. After Chamberlain.

spindle or "attached" at its centromere. The two limbs of the chromosome on either side of the centromere lie more or less accurately in the equatorial plane and may project outwards from the spindle into the cytoplasm. When the chromosomes have taken up this position they are said to have achieved "full metaphase." This affords the most favourable opportunity for counting the

chromosomes. To view the surface of the metaphase plate, a section must be prepared across the spindle. This lies with its long axis in the long axis of the cell, which in turn coincides with the long axis of the organ; root tips must therefore be cut transversely to see the metaphase plate in surface view (Fig. 28). Numerous observations of this kind show that the number of chromosomes is constant for any particular species and in flowering plants varies from six to over one hundred.

*Anaphase.*<sup>1</sup> The two halves of the chromosome now begin to separate. The first signs of separation appear at the centromere and the distal ends remain pressed together even though earlier on they may have separated for a time. Beginning at the centromere, the two

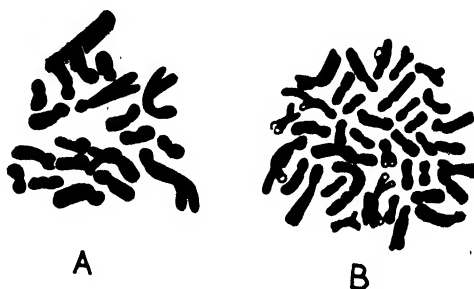


FIG. 28.—Metaphase plates of *Ruscus aculeatus* (butcher's broom). A, from pollen grain ( $n = 20$ ); B, from root tip ( $2n = 40$ ). The explanation of  $n$  is given in a later chapter. After Maude.

chromatids peel apart remaining together at the tips until the last moment (Fig. 25). The daughter chromosomes thus formed travel through the spindle towards the two poles. The spindle then elongates and contracts in the middle so that the two groups of chromosomes are finally pushed apart.

*Telophase.*<sup>2</sup> When the groups of daughter chromosomes reach the poles they first form a compact mass (Figs. 25 I and 27 E). They then begin to elongate again and their spiral form becomes more readily visible. They appear to pass through a series of changes similar to those of the prophase, but in reverse order. When these are complete, each daughter nucleus presents the same appearance as the parent nucleus before division began.

*Time-table of Mitosis.* The total time taken from the beginning to the end of mitosis appears to vary a good deal between different organisms. In the fruit fly *Drosophila*, it may be as little as ten

<sup>1</sup> Greek ἀνά (ana), again, anew.

<sup>2</sup> Greek τέλος (telos), end.

minutes; but in plant cells it may take several hours. The following are the times, in minutes, observed with living cells of two different species:

	<i>Prophase</i>	<i>Metaphase</i>	<i>Anaphase</i>	<i>Telophase</i>	<i>Total</i>
<i>Arrhenatherum</i> (grass)	36-45	7-10	15-20	20-35	78-110
<i>Tradescantia</i> (spiderwort)	181	14	15	130	340

Metaphase and anaphase are relatively fast; prophase and telophase relatively slow.

#### *Division of the Chromosomes and the Doctrine of Permanence*

According to the description just given, mitosis consists essentially of the separation of the two halves of chromosomes that are already divided. The question naturally arises, when does the actual division of the chromosomes take place? Since it cannot be seen to happen during any of the stages of mitosis, when the chromosomes are readily stainable and so easily made visible, it must presumably happen when they are more fluid and less open to inspection; that is to say during the so-called resting stage, obviously a misnomer. In some nuclei it may occur during the last stages of telophase, that is before the daughter nucleus is even fully constituted. In either case it is, of course, implied that the chromosomes are permanent structures, even though they cannot be demonstrated at all times. It will be shown in Chapter XXI that such an hypothesis is also extremely plausible and valuable in the study of heredity.

#### *Cell Division. The Formation of New Walls*

The division of the nucleus is normally the first step in cell division. As it approaches completion, cells without walls tend to elongate towards the poles and to form an equatorial constriction which closes in until the two daughter cells are entirely separate, though they remain pressed together. This type of division is characteristic of animal cells.

In walled cells, such as those of a root meristem, division is completed by the laying down of a new wall in the equatorial plane. As

the spindle is usually formed in the long axis of the cell, this means that the new wall forms across the short diameter. Division is into two equal parts. The new wall appears first as dot-like thickenings at the equator of the spindle which gradually coalesce into a thin continuous plate (Fig. 25 I-L). This plate is really double, having been formed in two layers, one from each daughter cell. It is composed of protein material and lies without tension in the protoplasm. Between the two layers thus formed the *middle lamella*, consisting of pectic materials (p. 78), is secreted and may perhaps be likened to the intercellular substances of animal cells. At a later stage layers of cellulose are deposited, the wall becomes thickened and elastic and, as the daughter cells enlarge, it takes up the same tension as the side walls with which it is associated (cf. Fig. 135, p. 217).

In some of the filamentous algæ, such as *Spirogyra* (p. 115) wall formation follows a different course. Instead of appearing first in the spindle material, the wall develops outside it, growing from the periphery inwards, rather like the closing of an iris diaphragm (Fig. 29). In this way the daughter protoplasts are nipped apart just as in the animal type of cell cleavage.

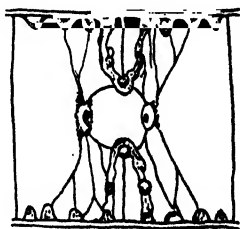


FIG. 29.—Wall formation following cell division in *Spirogyra maiuscula*. Nuclear division is complete and the new wall is closing inwards from the side walls.  $\times 160$ . After Strasburger.

#### *Development of the Adult Parenchyma Cell from the Meristematic Cell*

So long as cells remain meristematic they continue to maintain a rhythm of growth and division. The daughter cells on the side towards the body of a root or shoot gradually pass out of the meristematic state and assume the characters of permanent tissue cells. At the same time their ability to divide becomes much less and, with comparatively rare exceptions, is lost.

The permanent tissue cells commonly attain a size far greater than that of the meristematic cells. They frequently grow most in the direction of the long axis of the root, stem or leaf of which they are a part, and become several times longer than broad. This great increase in the size of the cell does not result from an increase of protoplasm but from the formation and increase in size of the vacuoles. Drops of liquid cell-sap appear in the endoplasm, increase in size and finally run together to form the large central vacuole (Fig. 23 B and C). During this development the nucleus, embedded in the

cytoplasm, remains suspended in cytoplasmic strands which still run across the centre. As these are thinned out and collapse, the nucleus is pressed with the cytoplasm outwards towards the cell wall.

The large increase in size of the vacuoles distends the cell wall, which is continually added to by new deposits of cellulose secreted by the protoplasm lining its inner surface. These depositions go on even after the extension of the cell is complete, so that the wall becomes noticeably thickened. Successive layers of thickening are often visible (Fig. 24 D). They are not necessarily continuous over the whole cell surface and channels or *pits* may be left leading from the middle lamella to the body of the cell. The pits of adjacent cells are practically always formed opposite to one another.

### *Water Relations of the Cell*

Unicellular organisms nearly all live submerged in water and the cells of the higher types are all bathed by watery solutions; body fluids, sap streams and the like. Their relations with the external water are dominated by the fact that protoplasts, or at least their superficial layers, are freely permeable to water itself, but much less permeable to substances dissolved in it. Membranes of this kind are described as semipermeable. The cell wall is a fully permeable membrane, because the colloidal micelles of its cellulose (p. 77) are relatively widely spaced in a continuous phase of water. Its principal importance lies in the fact that it has considerable elastic strength and so puts up a resistance to stretching. The semipermeability of the protoplasm may be limited to its two surfaces where it faces the cell wall outwards and the vacuole inwards; but for many purposes this makes little difference, and it is usually enough to think of it as a single semipermeable membrane.

Wherever solutions of two different concentrations are separated by a semipermeable membrane, water tends to pass through the membrane to equalise the concentrations. This is an example of *osmosis*<sup>1</sup> which in general is defined as the tendency of two miscible liquids to intermix. If some sugar solution is put into a parchment bag open at the top and partly immersed in a beaker of water, the volume of liquid in the bag increases. Water passes into the bag from outside, but no sugar solution escapes because the parchment membrane is semipermeable to a sugar solution. If common salt were used instead of sugar, the volume of solution in the bag would at first increase but afterwards diminish again because the salt penetrates the

<sup>1</sup> Greek ὥσμις (*ōsmis*), push.

parchment, though much more slowly than the water. Equilibrium would be reached when enough salt had escaped and enough water entered to make the concentrations equal inside and outside the bag. To make the system more like a cell the open mouth of the bag would have to be tied up. Then, as water entered, a hydrostatic *turgor pressure* would become apparent, distending the bag. It would be equal in magnitude and opposite in direction to the *wall pressure* developed by the parchment in opposition. In this model the parchment would provide both semipermeability and elastic resistance, but in the cell the two properties are divided between the protoplasmic lining and the cell wall respectively. Vacuoles arise as centres of liquefaction where soluble substances such as sugars and plant acids accumulate. These are unable to pass out through the semipermeable protoplasm and water enters from the diluter saps or soil solutions outside. This goes on until an osmotic equilibrium is reached. As water enters an enclosed vessel by osmosis a pressure is developed. The more numerous the solute particles, the greater is the pressure. It is therefore high in any ionised salt solution and is low in colloidal sols where the dissolved matter is collected into relatively few and large particles. The maximum pressure developed by any given solution is called its *osmotic pressure*. A cell immersed in pure water would reach equilibrium when the wall was so distended that the resulting wall pressure exactly equalled the osmotic pressure of the solution in the vacuole. In the more usual condition where the outside solution also contains some solutes, water is absorbed until the osmotic pressure of the vacuole is equalled by the wall pressure plus the external osmotic pressure. Putting it a little differently, the cell's power to absorb water, often called its suction pressure, is equal to the vacuolar osmotic pressure minus the wall pressure. When this difference is reduced to the level of the external osmotic pressure, no more water enters the cell. The suction pressure is reduced as water enters, both because the vacuolar solution is diluted and because the wall pressure is increased by the extra stretching. In a tissue where the cells are surrounded on all sides by other cells, the pressure due to their pushing against one another also opposes the osmotic intrust.

The normal distended condition may be artificially altered by putting a cell or tissue into a sugar or salt solution stronger than the solution in the vacuole. Osmotic pressures are additive, and it does not much matter what substance is used so long as the membrane is semipermeable to it and is not damaged by it. Immersed in the

strong solution the cells lose water from their vacuoles; they contract and finally the protoplasm shrinks away from the cell wall as this reaches the limit of its contraction. The cell is then said to be *plasmolysed*<sup>1</sup> (Fig. 30 B). If a series of sugar solutions of varying concentrations were employed, it would obviously be possible to find one with a concentration just equal to the strength of the vacuolar sap. In this the cell wall would not be forcibly distended, nor would the protoplasm shrink away from the cell wall (see Exp. 10, p. 63). A solution which just fails to cause plasmolysis is said to be isotonic<sup>2</sup> with the cell sap. This equality only holds at the "threshold of plasmolysis," since the concentration of the cell sap itself varies as water is taken up or lost. Plasmolysis also provides direct evidence

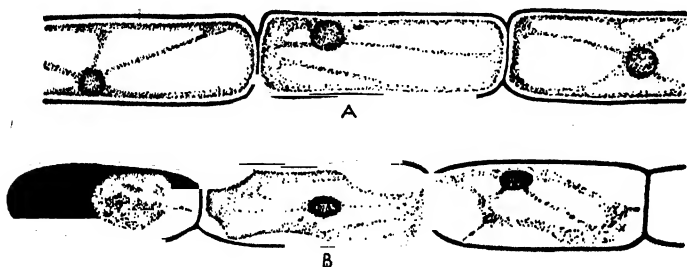


FIG. 30.—Cells from the hairs on the stamens of *Tradescantia virginica*. A, normal condition. B, plasmolysed.

that the cell wall is freely permeable and that semipermeability is limited to the protoplasmic lining. If it were not so the whole cell, wall and all, would buckle up when placed in a hypertonic<sup>3</sup> solution, and this is precisely what happens to the cells of some mosses which do possess semipermeable walls.

With the usual type of cell it will also be possible to find a solution which neither gives water to the cell nor takes any away from it. This can be determined by measuring the cell, or piece of homogeneous tissue; or, with the tissue, by weighing it. If there is no change, the suction pressure (osmotic pressure less wall pressure) is equal to the osmotic pressure of the external solution. It will clearly always have a lower value than the osmotic pressure "at threshold plasmolysis."

<sup>1</sup> Greek λύσις (lusis), loosening of the plasma from the wall.

<sup>2</sup> Greek ἴσος (isos), equal; τόνος (tonos), thing stretched.

<sup>3</sup> Greek ὑπέρ- (huper-), above, or exceeding.

### *Turgor*

When a cell is not plasmolysed but is distended by the pressure of its vacuolar sap upon the containing cell wall it is said to be in a state of turgor. Turgor is the natural condition of all living and vacuolated plant cells and without it normal growth does not occur. Temporary plasmolysis may not do any permanent harm, but the natural formative processes will only go on in stretched and turgid cells. The maintenance of turgor due to the cell structure and its relations with water is therefore a physiological process of considerable importance. In complex plants it has yet another result in establishing the erectness and firmness of the tissues of young and soft organs such as stem and root tips and leaves. This is well illustrated by the behaviour of a piece of rhubarb in which a central cylinder of tissue is freed by cutting it out with a cork borer. If both pieces are immersed in water for half an hour, it will be found that the central cylinder can no longer be fitted into the hole from which it came. It is composed of comparatively large vacuolated cells which have taken up more water and stretched their walls in doing so. The cylinder has not much mechanical strength and some care is necessary not to break it. The outer jacket, on the other hand, has remained firmer and swollen less. Two components obviously contribute to the firmness of the original stalk, (a) the turgor of the inner parenchyma pressing outward against the tough skin of the outer tissues, and (b) the inward squeeze of the surface tissues (outer cortex) which are composed of smaller thicker-walled cells without intercellular spaces. It is the balance of these two opposed pressures which produces the rigidity and is comparable to the effect produced within a single cell, but carried out on a higher level of structure.

A converse experiment may also be carried out by immersing any young stalk in a strong salt solution, when it soon becomes flaccid owing to the plasmolysis of its cells and the consequent disappearance of their outward thrust against the superficial tissues.

## **Practical Work**

### THE PLANT CELL

(1) The "flesh" of many fruits consists of a loose parenchyma, and individual cells can easily be teased out with needles for study. Suitable fruits are privet, snowberry, tomato, gooseberry, "mealy" apples or other fruits in season. Tease out a little of the pulp into a drop of water on a slide and see that it is well wetted. Note that the tissue is loose with large intercellular spaces between the more or



less spherical walls. All the centre of the cell is occupied by the *cell sap* (coloured, in privet). Look for the *cytoplasm* pressed against the thin *cell wall*, and the *nucleus*. Add a little dilute iodine to make them more visible. Coloured *plastids* may also be visible in the cytoplasm, e.g. orange chromoplasts in tomato or green chloroplasts in privet.

(2) Strip off the surface layer of cells from the inside of an onion bulb scale and mount in water. Examine and draw carefully under the high power. The cells are elongated in the direction of the long axis of the bulb scale. Note the *vacuole*, *cytoplasm* and conspicuous *nucleus* with one or more *nucleoli*. Run in iodine afterwards to make the nucleus clearer; but observe it carefully first.

(3) The hairs growing from the surface of young parts of plants afford useful material. They usually consist of a single cell or a row of cells. The hairs on the stamens of *Tradescantia* (spiderwort) species are particularly interesting and are obtainable from most large gardens. Mount a hair in a drop of water, cover and examine first under the low and then under the high power. Note the colourless *wall*, the purple *cell sap*, the *cytoplasm* which lines the wall and also has numerous strands (bridles) running across the *vacuole*. Find the *nucleus*. The protoplasm will probably show active streaming both at the sides and along the strands. Kill the cell by irrigating a little alcohol under the coverslip. The streaming stops, and the coloured cell sap oozes out. The alcohol coagulates the protoplasm and thereby destroys its semipermeability, allowing the pigment to escape.

#### DEVELOPMENT

Prepared slides of longitudinal sections of bean root tips, suitably stained, are required for this section and are readily obtained from botanical suppliers.

(4) Examine the slide under the low power. Locate the position of the *meristem* just behind the extreme tip which is formed by a parenchyma, the *root cap*. (a) Focus the meristem under the high power and draw a small group of its cells, noting the large *nucleus*, with *nucleoli*, the granular *cytoplasm* and the thin *cell walls*. (b) Move the slide to bring cells rather higher up the root into view. Observe and draw successive stages of vacuolation and elongation which occur in the direction of the main axis of the root.

#### MITOSIS

(5) Examine the longitudinal bean root section for nuclei showing stages of mitosis. Several such stages are likely to be found. Identify and focus them under the best magnification obtainable. Make a series of drawings, arranging them in the proper sequence.

(6) Examine similarly a transverse section across the meristematic region of a bean root tip. Find one or more metaphase plates; draw and estimate the number of chromosomes (12 or 14).

It is a help if demonstration slides mounted under oil-immersion lenses are available for (5) and (6).

#### WATER RELATIONS OF THE CELLS

(7) Cut turgid bean or pea roots from seedlings raised in sawdust. Put samples (a) into water; (b) into M/2 (half molar) calcium chloride solution; (c) lying exposed on the bench. After a short time note that (b) and (c) become flaccid, while (a) remains turgid. Put (b) and (c) into water and examine later to see if turgor is regained.

(8) Using a sharp knife, split a fresh young bean stem or dandelion stalk longitudinally into quarters. Note that the ends of the strips curve outwards owing to the expansion of the inner cells when they are released from the compression of the outer tissues. Immerse pieces in M/2 calcium chloride and note that the

curvature is straightened or reversed. Why? Alternatively, perform the experiment with rhubarb stalks described in the text on p. 61.

(9) Mount a cell or young group of cells having coloured sap in M/2 calcium chloride and keep under observation with the high power. The cells will be seen to plasmolyse, i.e. the protoplasm shrinks away from the walls and the coloured sap is reduced to a ball in the centre of the cell. Irrigate pure water under the coverslip to wash away the calcium chloride. Turgor will slowly be regained. Suitable cells may be obtained from lower epidermis of *Rhæo discolor*, privet berries, staminal hairs of *Tradescantia*, washed sections of beetroot, flower petals and from many other sources.

(10) Given a molar solution of sucrose, prepare a series M/2, M/4, M/6, M/8, M/10 by dilution with distilled water. Prepare a number of pieces of any one of the above tissues and place two or three in each solution in a watch glass, preferably covered. After about half an hour, transfer the tissue pieces in drops of their own solutions to slides and examine under the low power. Decide the solution in which the majority of the cells just fail to show plasmolysis. This is isotonic with the average cell sap. Assuming the osmotic pressure of molar sucrose to be 34.5 atm., calculate the osmotic pressure of the average sap.

## Chapter V

# THE GREEN CELL : PHOTOSYNTHESIS

The green cell, green, that is, because of its possession of *chlorophyll*, is the speciality of the plant world. It is unique in the way in which energy and material are built into it. The raw material which it uses is entirely inorganic, consisting of carbon dioxide and water ; and in this it differs sharply from animal cells which depend on the products formed by green plants for their energy, growth and maintenance. Colourless plants resemble animals in this respect and are called *heterotrophic*<sup>1</sup> to distinguish them from the self-supporting green plants which are called *autotrophic*.<sup>2</sup> Plants possessing green cells are not always green to outward appearance, since their chlorophyll may be masked by other pigments ; brown in the brown seaweeds, coppery in copper beech and so on. Plants with silvery foliage usually have their greenness masked by numerous fine hairs interweaving over the leaf surface.

The process by which carbon dioxide and water are built into the plant is called *photosynthesis*<sup>3</sup> because it only occurs under the influence of light. The products of photosynthesis contain more energy than the carbon dioxide and water from which they are formed, and the excess is obtained from sunlight. The colourless protoplasm itself naturally traps very little of the light which falls upon it, but the opaque chlorophyll traps all except the green component which escapes and gives the tissues their green appearance.

### *Chlorophyll and Chloroplasts*<sup>4</sup>

Chlorophyll is a mixture of four pigments. They are all insoluble in water but give solutions of different colours in organic solvents, such as ether. The four are—chlorophyll *a*, blue-green solutions ;

<sup>1</sup> Greek ἕτερος (heteros), the other ; τροφή (trophe), food.

<sup>2</sup> Greek αὐτός (autos), self.

<sup>3</sup> Greek φῶς, φως (phōs), light ; σύνθεσις (sunthesis), a putting together.

<sup>4</sup> Greek χλωρός (chlōros), green.

chlorophyll *b*, pure green; carotin, orange; and xanthophyll, yellow. The mixture usually contains about three molecules of the green pigments to one of the yellow. They are not distributed throughout the protoplasm, but are confined to special bodies, the *chloroplasts*, which are embedded in the cytoplasmic lining of the cell wall (Fig. 31). Green cells always possess a nucleus, but owing to the abundance and bright colour of the chloroplasts it is often difficult to find it. The chloroplasts of the higher plants are usually small and bun-shaped (Fig. 31); but among the simpler plants they are often fewer in the cell and of many diverse forms. A range of examples may be observed in *Protococcus* (p. 22); *Euglena* (p. 23); *Chlamydomonas* (p. 98); and *Spirogyra* (p. 116). Whatever shape is assumed, the chloroplasts are invariably found closely appressed to the cell wall which is always thin. *Euglena* is exceptional in having chloroplasts but no true cell wall.

Even within the chloroplasts chlorophyll is not evenly distributed, but is located in *grana* probably about  $1\ \mu$  across (Fig. 32). It is here probably attached to special proteins in somewhat the same way that the blood pigment is attached to the protein of hæmoglobin, though with a rather weaker linkage.

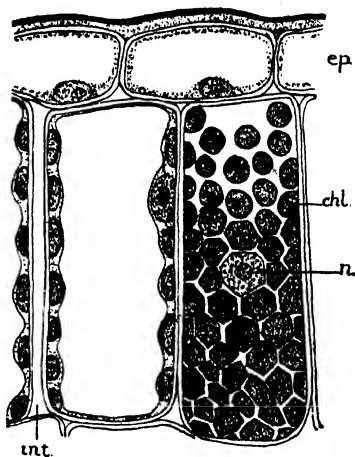


FIG. 31.—Two palisade cells. The one on the left is seen in optical section and the one on the right in surface view; *chl*, chloroplast; *n*, nucleus; *int*, intercellular space; *ep*, epidermis.

### *Chlorophyll and Light*

If a beam of white light is split into its various components by being passed through a prism, and is then passed through a solution of chlorophyll, it will be found that only some of the colours come through. In place of others there are dark gaps, the absorption bands, because these colours have been absorbed and retained by the chlorophyll. Chlorophyll has strong absorption in the red, orange-yellow and blue regions of the spectrum; but very little in the yellow-green (Fig. 33). The absorption spectrum of a living leaf, or suspension of unicellular green plants, is very similar to that of a solution of



*External Factors Affecting Photosynthesis*

The raw materials of photosynthesis are carbon dioxide and water. The latter is abundantly present in all living cells for reasons explained in the last chapter. Carbon dioxide enters from the air or water in which the plant exists. It is usually present only in traces, 3 parts in 10,000 of air, and is absorbed with a very high degree of efficiency. Apparently only carbon dioxide,  $\text{CO}_2$ , is absorbed, carbonates and organic compounds only being important in so far as they give rise to carbon dioxide itself. Raising the concentration of carbon dioxide increases the rate of photosynthesis within limits, always assuming that other requirements are adequately provided for. Similarly, raising the intensity of light falling upon the plant is likely to increase the rate; but a limit is eventually reached either because other factors are inadequately provided for, or—if they are all abundantly present—because the system becomes “light saturated” and cannot be driven faster.

Temperature also exercises an effect upon the rate of photosynthesis which, again, only becomes apparent when light and carbon dioxide are both plentiful. This dependence upon temperature is important because it indicates that photosynthesis includes chemical reactions of the normal type dependent upon heat energy, as well as its special reactions sensitive to light.

*The Stages of Photosynthesis*

At the present time it is not possible to describe all the chemical steps by which carbon dioxide and water are converted into products of photosynthesis. They have turned out to be very complicated and difficult to unravel. Some things can, however, be said about them which are worth knowing, and, for this purpose, it is convenient to recognise four successive stages.

*Diffusion Stage.* The structure of leaves and other photosynthesising bodies makes it clear that diffusion must inevitably be part of the process. Carbon dioxide may be wind-blown to the surface of the leaf, but the last stages of its entry through cell walls must be by the slow method of diffusion through their watery phase. The distance to be traversed in this way is very short, say about  $1\ \mu$ , and there is usually a large surface over which entry goes on.

*Combination Stage.* It is now known that when carbon dioxide gets into a cell it combines with some unknown substance very strongly. This is not chlorophyll, and may even exist outside the

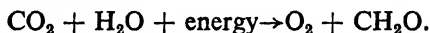
chloroplast in the cytoplasm. The combination occurs in dark as well as in light and is therefore not a photoreaction.

*Photostage.* In this stage the light absorbed by chlorophyll provides the energy to reduce carbon dioxide to photosynthetic products. It probably operates not upon free carbon dioxide but upon the "carbon dioxide complex" formed in the combination stage. Several light-activated reactions occur one after the other before the reduction is complete.

*Dark Stage.* The photoproduct of the previous stage is broken down by normal chemical reactions. A molecule of oxygen is released for every molecule of carbon dioxide absorbed. It has been shown by using heavy oxygen as tracer that all the oxygen comes from the water and none from carbon dioxide. The hydrogen of the water is used to reduce the carbon dioxide to the final product which remains within the plant.

### *The Products of Photosynthesis*

The simplest way in which the overall equation for photosynthesis can be written is:



The last formula on the right could stand for formaldehyde. Many attempts have therefore been made to identify formaldehyde in illuminated green cells, so far without definite success. It is possible that the first *free* product of photosynthesis is a sugar such as glucose or fructose with a common formula  $\text{C}_6\text{H}_{12}\text{O}_6$ , i.e. a six-fold polymer. Both these sugars, together with sucrose, accumulate during photosynthesis.

### *Formation of Starch in the Chloroplasts*

In most green cells sugar does not accumulate indefinitely but, after a certain concentration is reached, is further condensed to starch which appears as fine grains inside the chloroplasts. Starch formation is a sequel to photosynthesis rather than a stage of it; and, given enough sugar goes on even in the dark. The function of chloroplasts as starch formers is therefore quite distinct from their function as sugar producers. The leaves of many plants do not form starch at all, and the concentration of sugars necessary for starch formation varies considerably in different species. The power of forming starch from sugar is shared by the colourless plastids (leucoplasts)<sup>1</sup> found in colourless cells, especially in seeds, tubers and storage tis-

<sup>1</sup> Greek λευκός (leucos), pale.

sues generally. In such tissues large quantities of starch are formed from the sugar which comes to them from the leaves.

### *The Significance of Photosynthesis*

Nearly all the natural processes that affect the carbon atom tend to increase its state of oxidation. In all such reactions energy is transformed and some part of it is always dissipated as heat. The final step in this sequence is the formation of carbon dioxide and the carbonates. The carbon atom is then oxidised to the fullest extent possible and the maximum degradation of energy to heat has also occurred. The burning of all kinds of fuel—coal, oil and wood; the respiration of micro-organisms, plants, animals and man; and volcanic eruptions are all massive examples of the degradation of organic carbon to carbon dioxide. Fermentations, putrefactions, hardening of paints and varnishes, the formation of cuticles are a few examples of partial steps in the same direction. The amount of carbon existing on the face of the earth is large but not limitless, and the common direction of all these great natural events would sooner or later bring it all to a single form incapable of further change, and incapable, therefore, of being the vehicle of life. The only process which opposes this tendency on any large scale is the photosynthesis carried on by green cells. By photosynthesis carbon dioxide is reduced to organic carbon in the form of sugars and their derivatives and becomes once more capable of oxidation. Photosynthesis is, therefore, solely responsible for the maintenance of the upward limb of the natural *carbon cycle*, and is recognised as the most remarkable of all its amazing features.

Although the carbon cycle is reversible, the energy changes are not. There is no way in which the energy that has been converted to heat and dissipated to the surrounding temperature level can reconvert itself to energy of chemical linkages in sugar and other molecules. The energy responsible for the photosynthetic reduction of the carbon dioxide is a new importation; it is the energy of light newly arriving from the sun, and only by its continuous acquisition is the terrestrial carbon cycle kept in operation.

## Practical Work

### CHLOROPLASTS AND CHLOROPHYLL

(1) Mount a leaf of the water plant *Elodea canadensis* or a moss "leaflet" in a drop of water. Cover and examine under the microscope. Both these organs consist of thin laminae of green cells of simple structure. Note the abundant chloro-



*plasts* and show by careful focusing that they are all pressed against the walls of the cells. The centre is occupied by a colourless *vacuole*. The chloroplasts are embedded in the peripheral *cytoplasm* which, especially in *Elodea*, may often be seen streaming round the cell carrying the chloroplasts with it. The *nucleus* is usually rather difficult to detect among the more obvious chloroplasts.

(2) Chop up a handful of grass-cuttings and put into a flask with about 100 ml. of 85 per cent. acetone. Allow to stand with occasional shaking until the colour has passed into the acetone. The extraction may be made more rapid by placing the finely chopped grass in a Buchner funnel and drawing the acetone through several times and by carefully drying the grass at low temperatures beforehand. When the acetone has become deep green, a blood-red fluorescence characteristic of true solutions of chlorophyll will be visible.

(3) Drop a spot of the solution on to a clean piece of filter paper followed by several others in exactly the same position. Follow with a few drops of acetone. As the pigment spreads itself, notice the yellow pigments travelling farthest and forming narrow circles of red (carotin) and yellow (xanthophyll) round the green chlorophylls.

A better separation can be shown as follows: Put about a quarter of an inch depth of the mixed chlorophyll extract into a beaker or saucer and stand a new piece of "blackboard chalk" upright in it. When the pigments have risen half an inch or so, develop the bands by replacing the solution round the base of the chalk column with acetone. From above downwards there will be visible bands of carotin, xanthophyll, chlorophyll *a* and chlorophyll *b*.

(4) Expose leaves of *Pelargonium* (garden geranium) of the variety with a white edging to the leaf, to a bright light for two or three hours. The petioles should dip into water to prevent wilting. Take a leaf, soak it thoroughly in water, lay under a piece of glass and take a tracing on transparent paper of the green and colourless portions. Then dip the leaf into boiling water and decolorise it in a beaker of boiling 70 per cent. alcohol. The beaker should stand in a water bath which has been brought to the boil previously and the flame then extinguished. The fumes from the boiling alcohol are highly inflammable. Place the brittle leaves on a saucer and soften with water. Pour off the water and replace it with a solution of iodine in potassium iodide. When there are no further colour changes, wash away the iodine with several rinses of water. Compare the presence of the blue-black starch-iodine colour with the original tracing.

(5) Detach a few *Elodea* or "moss" leaflets that have been well illuminated and immerse in a solution of chloral hydrate (160 gm. mixed with 100 ml. distilled water) tinted with a few drops of iodine solution. The chloral hydrate clears the leaf by dissolving the protoplasm. Note that starch grains are present in the chloroplasts. If they cannot be seen clearly, decolorise some leaves with hot alcohol, as in (4) and repeat.

(6) Mount a cross-section of a fresh *Pellionia* stem in water and examine under the high power. The cells near the surface of the stem have large chloroplasts with bright colourless starch grains which may become so large as to burst the chloroplasts. Draw examples of various stages in the development of the grains and test with iodine solution to verify the presence of starch.

(7) If a hand or other spectroscope is available, examine and compare the absorption spectra of your mixed chlorophyll extract and that of any thin green leaf. See Fig. 33, p. 66, for the principal absorption bands.

#### CARBON DIOXIDE

(8) Put a pot plant of *Pelargonium* for two days in the dark, by which time starch will have disappeared from its leaves. Test a young leaf as in experiment (4) to make sure no starch remains. Take two 250 ml. conical flasks and put about 20 ml. of strong caustic soda in one and water in the other. Introduce a young

detached leaf into each flask, making sure that the caustic soda does not come into contact with it. Cork tightly and keep in the light for several hours; then test the leaves for starch. If carbon dioxide has been properly excluded there will be no starch formation. The control over water should show starch.

#### LIGHT

(9) Make a small envelope of dull black paper and cut out a simple design on one face. Fix it on to a leaf without starch prepared as in (8). Fasten it on securely with paper clips so that no light can get between the leaf and the dark paper. Expose to a bright light for about four hours and then test for starch as before. Only the part where the envelope was cut will show starch formation.

This experiment may be more elaborately performed if a large leaf is used and sufficient opening made in the envelope to accommodate a photographic negative. A good print may be developed on the leaf with iodine after exposure.

#### REDUCING SUGARS

(10) Cut up a leaf that has been exposed to bright light and crush it well with water. Filter off a little of the liquid into a test tube. Add about 3 ml. Fehling's solution (p. 83) and boil. The formation of a brick-red precipitate indicates the presence of a reducing sugar such as glucose or fructose.

## Chapter VI

### ORGANIC SUBSTANCES AND THEIR CHEMICAL CHARACTERS<sup>1</sup>

All the activities of life depend upon protoplasm which is therefore the essential part of every living organism. But by no means all *parts* of an organism consist of or contain living protoplasm. For instance, the heartwood and outer bark of a tree, and the hairs, feathers, nails and hoofs of a warm-blooded animal are destitute of protoplasm. These lifeless parts of an organism are, however, all formed by or from protoplasm and they consist mainly of complex chemical compounds containing *carbon*, *hydrogen* and *oxygen*, often also *nitrogen* and *sulphur* as well as other elements. They are called "organic" compounds because they are associated with organisms. There is no sharp distinction between organic and inorganic substances in chemistry, and many of the simpler organic compounds formed by organisms can also be made synthetically in the laboratory.

All the organic compounds contain the element carbon, organic chemistry being often defined as the "chemistry of the carbon compounds." Carbon is unique among elements in the enormous number and variety of more or less stable compounds which it can form; over 100,000 are known. Even silicon, its neighbour element that plays a part in geology almost approaching that of carbon in biology, falls very far short of its versatility. The reasons lie in the properties of the carbon atom such as its tetravalency enabling each atom to combine with as many as four others; its sluggishness (so that compounds once formed do not readily break up); the unusual strength of the carbon-carbon bond that enables it to build up stable chains of enormous length; its evenly balanced affinities enabling it to form compounds of reasonable stability with a wide range

<sup>1</sup> Some background knowledge of elementary organic chemistry is necessary in reading this chapter. It is impossible to understand certain aspects of biology without such collateral knowledge.

of other elements. Its affinities for oxygen and hydrogen are so nearly balanced that oxygen of the air is not usually able to break its link with hydrogen, and organic compounds are stable in air.

Of the immense number of carbon compounds known, certain classes are especially important in the structure and activities of living organisms, and we must have some knowledge of their nature and properties before we can hope to understand anything of protoplasm. It is necessary in the first place to distinguish between an organic substance which is a mixture of chemical compounds in various proportions and a chemical compound which has a perfectly definite chemical composition, i.e. its molecule or ultimate element of structure consists of a definite number of atoms of different elements arranged in a definite way. Milk, for instance, is an organic substance which has a varying composition, being a mixture in various proportions of the chemical compounds, water, milk sugar, various definite fats, proteins, salts, etc. Protoplasm is itself a mixture of great complexity.

#### *Inorganic Constituents of Protoplasm*

Protoplasm contains many inorganic substances which are an essential part of its make-up; but which remain unaltered in the same chemical form in which they were absorbed. Potassium and phosphate ions are notable examples. The most important of the inorganic substances in protoplasm is *water*. It is essential to the structure of living protoplasms and is found in a greater or less proportion in all parts of the body. More than 80 per cent. of the weight of a herbaceous plant is water, as can easily be shown by weighing the plant, heating it at 100° C. till it loses no more water, and then weighing again.

The three classes of organic compounds which play the leading part in organisms are the *carbohydrates*, the *fats* and the *proteins*; the two former consisting of *carbon*, *hydrogen* and *oxygen*, the last with *nitrogen*, *sulphur* and sometimes *phosphorus* in addition.

#### *The Carbohydrates*

These are a class of compounds in whose molecules the atoms of hydrogen and oxygen are generally present in the proportion of two to one, as in water. They are not simple hydrates of carbon. The simpler carbohydrates behave as aldehydes or ketones, i.e. they have important reducing properties; and also as alcohols by combining

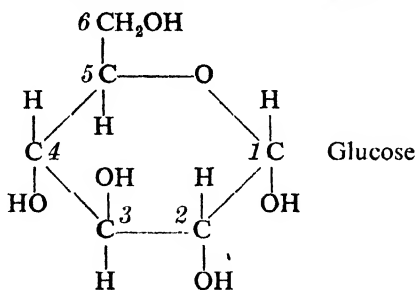
with phosphates and other acid radicles to form esters. The common carbohydrates are classified as follows:

1. *Sugars*

{	Monosaccharides	Pentoses ( $C_5H_{10}O_5$ ), e.g. arabinose, xylose.
		Hexoses ( $C_6H_{12}O_6$ ), e.g. glucose, fructose.
	Disaccharides	( $C_{12}H_{22}O_{11}$ ), e.g. sucrose, maltose.
2. *Polysaccharides*  $C_n(H_2O)_{n-1}$ , e.g. starch, cellulose, hemicellulose, gums, mucilages, pectic materials.

**THE SUGARS.** The simpler carbohydrates are called sugars. They are all very readily soluble in water, giving colourless solutions of varying degrees of sweetness. The termination *-ose* is used to indicate them. Although there are only three molecular formulæ given above for sugars, there are many natural and artificial sugars corresponding with each formula and differing from one another in the ways in which the atoms are grouped within their molecules.

*Monosaccharides. Glucose and Fructose.* Monosaccharides with five carbon atoms in their molecule are called *pentoses*. They have the usual properties of reducing sugars (see below). They rarely occur free in plants but are invariable constituents of many polysaccharides. *Hexoses*, with six carbon atoms in the molecule, include the important representatives glucose (grape sugar) and

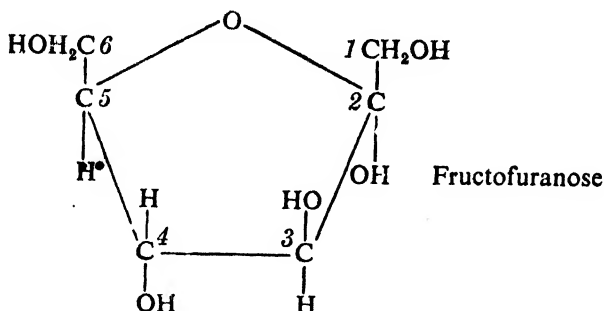


fructose (fruit sugar). The glucose molecule has been much studied in recent years and is believed to be shaped like a flat hexagonal plate with H atoms and —OH radicles disposed above and below the plate. Its approximate size is  $0.6 \times 0.5 \times 0.15 \text{ m}\mu$ .<sup>1</sup>

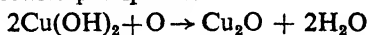
The fructose molecule is somewhat similar. Combined fructose also exists in plant materials in an active, fructofuranose, form which has a five- instead of six-membered ring.

<sup>1</sup> The millimicron ( $\text{m}\mu$ ) =  $1/1,000,000$  of a millimetre.

When the glucose ring opens it forms a chain with a terminal reducing group, -CHO and is therefore called an aldehyde sugar, or aldose. The corresponding fructose chain has its reducing group,  $>\text{CO}$ , in the second position, and is a ketone sugar, or ketose.



The reducing power of sugars is particularly marked in strongly alkaline solutions and the identification of a "reducing sugar" depends mainly upon this property. Fehling's, the commonest form of this test, consists of the reduction of cupric hydrate, a deep-blue solution, to cuprous oxide, a red precipitate, in the presence of alkaline tartrate. The tartrate serves to bring into solution the cupric hydrate which would otherwise precipitate.



(see also Exp. (1), p. 83).

Outside living cells monosaccharides are stable substances and, when solid or in pure and uninfected solutions, will remain unchanged for years. Atmospheric oxygen will not bring about their oxidation spontaneously. Inside plant and animal cells they come under the influence of catalysts (see enzymes, p. 81) that facilitate their reactions and they become liable to three principal types of change:

1. They are readily broken down to simpler substances. This breakdown, or glycolysis, followed by oxidation of its products, results in the transformation of much free energy which thus becomes available to do work or effect changes inside the organism.
2. Their molecules are *condensed*, i.e. combined with the loss of water, so forming disaccharides and polysaccharides.
3. They combine with non-sugar molecules to form a great variety of substances called *glycosides* and *esters*.

Reactions of type 1 are the basis of respiration; and reactions of types 2 and 3 contribute to the syntheses of growth.

**Disaccharides. Maltose and Sucrose.** The common disaccharides are all formed from hexose and none from pentose units. They may retain some of the reducing power of their constituent monosaccharides: *maltose*, a glucose disaccharide extracted from sprouting barley grains (malt) is the best-known example. *Sucrose* (cane sugar), the most abundant of all the natural sugars, is a disaccharide of glucose and fructose. It has no reducing power because the reducing groups of both its hexose constituents are involved in the condensation linkage. It is therefore a relatively inert substance but is much more easily hydrolysed than maltose by boiling with dilute acids because its fructose is in the active furanose form. On

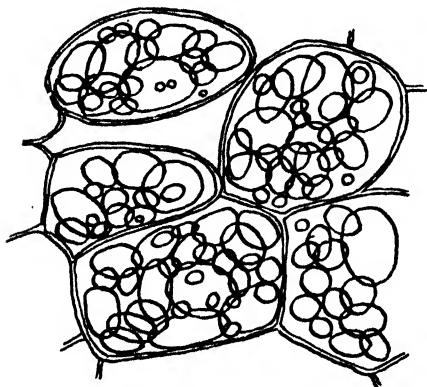


FIG. 34.—Starch grains in potato cells.  $\times$  about 300.

release, the fructose spontaneously adjusts its ring to the stable six-membered pyranose form.

The detection of sucrose is carried out by first hydrolysing, i.e. splitting the molecule by reaction with water, and then ascertaining the presence of the reducing sugars.

Sucrose is the main product of sugar canes and sugar beet in which it may amount to a fifth of the

total weight. It is the sugar of everyday use. It is sweeter than glucose, but the latter is sometimes recommended for the use of children and invalids as being more readily digested.

**POLYSACCHARIDES.** The polysaccharides differ from the sugars by being increasingly insoluble in water. They are derived from monosaccharides by the condensation of numerous molecules, from about six in a simple dextrin to about two hundred in cellulose. Glucose is by far the commonest parent sugar and the insolubility increases with the size of the polysaccharide molecule.

*Starch* (Fig. 34) is formed as grains in special regions of the protoplasm called amyloplasts. The substance of each grain is laid down in concentric layers round a centre called the hilum. The exact form of the completed grain depends on the plant from which it comes. With sufficient practice it is possible to distinguish the starch grains of one species from those of any other. It is thus possible to say with

certainly whether wheat flour, for example, has been adulterated with meal from any other source.

A complete starch grain contains two substances. *Hexa-amylose*, the simpler constituent, is formed by six glucose molecules with the elimination of five molecules of water. *Amylopectin*, the second compound, is a much more complicated substance and is believed to contain numerous hexa-amylose units in its molecule, the nature of their combination being uncertain.

Starch has a very characteristic blue reaction with a watery solution of iodine in potassium iodide. In the absence of water, e.g. with a solution of iodine in alcohol ("tincture of iodine") there is no reaction. Starch is quite insoluble in cold water and forms a paste when boiled. It is hydrolysed by boiling with dilute acids or by the action of the enzyme *amylase*. Simpler soluble polysaccharides called dextrins, which give a purple colour with iodine, are formed as intermediates and the final product of acid hydrolysis is pure glucose. Starch may also be broken down by the enzyme *phosphorylase*, and then the product is a phosphate ester of glucose—glucose-1-phosphate.<sup>1</sup>

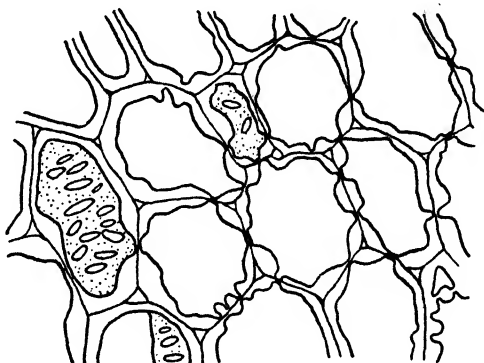


FIG. 35.—Cells from the seed of white lupin showing the hemicellulose thickenings of the walls. Some cells show lower walls with pits in surface view.  $\times$  about 250.

*Cellulose* is a very characteristic product of plants, being formed by them in vast quantities and not formed at all by animals. It is very resistant and, once formed, is only broken down by certain cellulose-destroying bacteria. No other plants can utilise it as a food-stuff, though the related *hemicelluloses* formed from sugars other than glucose, are often laid down in seeds and serve to nourish the young seedlings (Fig. 35).

Cellulose is not precipitated like starch as grains within the protoplasm, but is laid down as a continuous membrane at the sur-

<sup>1</sup> In this and similar names the figure indicates the number of the carbon atom (see sugar formula, p. 74) to which the non-sugar is attached.



face of the cell and forms the bulk of the cell wall. The hemicelluloses accompany it in this position.

The cellulose molecule has a most unexpected shape. It is formed from *cellobiose*, a disaccharide of glucose that differs only very slightly from maltose. About sixty cellobiose units are linked up end to end in a long straight chain that forms the cellulose molecule. These long threadlike molecules do not exist independently but in the natural condition as in the cell wall are loosely joined side by side into bundles, or *micelles*. The space between the bundles is always occupied by water.

True cellulose does not itself give a blue colour with iodine but, after treatment with strong acids, it forms a substance called "*amyloid*" that does. This reaction is generally used, especially for microscopic purposes, in the form invented by Schultze (Exp. (4), p. 83).

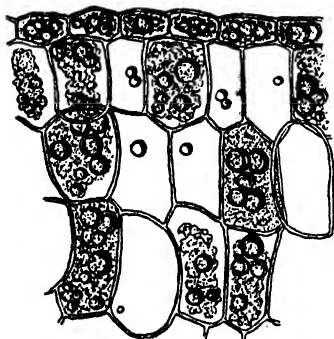


FIG. 36.—Cells from a sunflower seed showing drops of oil in the cytoplasm.  $\times$  about 250.

Cellulose is of immense importance because, being the main substance of the cell walls, it forms the "skeleton" of the plant. Linen and cotton are nearly pure cellulose and paper contains a varying amount according to the plant substance from which it is made; the purer the cellulose the better the

paper. Modified cellulose, prepared by various treatments of natural cellulose, include rayon ("artificial silk"); photographic film (cellulose acetates); guncotton and celluloid (nitro-celluloses); cellophane, sausage skins, etc.

Other polysaccharides, *gums*, *mucilages* and *pectic substances*, are mixed polysaccharides containing pentose sugars as well as glucose. Glycogen, which replaces starch in yeast and animals, is a glucose polysaccharide with a smaller molecule than starch. It gives a purple colour with iodine and is soluble, and so resembles a dextrin. *Inulin* is a simple polysaccharide of fructose which replaces starch in some plants.

### The Fats

These, like the carbohydrates, consist of carbon, hydrogen and oxygen, but the fat molecule is much larger than the sugar molecule and contains a much smaller proportion of oxygen. On oxidation fats therefore consume more oxygen and also liberate more energy

than an equal weight of sugar. Nearly all plant fats are liquid at ordinary temperatures and are commonly called oils. They are immiscible with water but form fine emulsions with it if vigorously shaken. They mix freely with organic solvents such as ether and are stained by dyes such as Sudan III, which are less soluble in water (see Exp. (6), p. 84). Chemically they are esters of glycerol and various organic acids. Two examples are palmitin ( $C_{51}H_{98}O_6$ ) from palm kernels and triolein ( $C_{57}H_{104}O_6$ ) from olives. The fats are widely distributed in plant cells where they occur as droplets or emulsions in the protoplasm. They occur in specially large quantities in the reserve tissues of many seeds, such as castor oil, coconut, linseed, sunflower, etc. (Fig. 36). *Cutin*, which covers the outer surface of plants in a thin layer called the cuticle (Fig. 37), and *suberin*, which occurs in cork cells, are complex oxidation and condensation products of the fats.

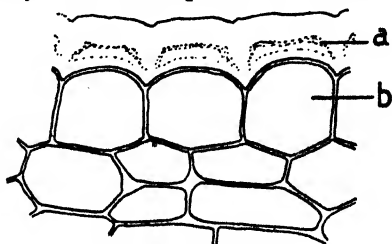
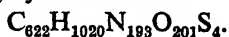


FIG. 37.—Epidermal cells of a stem. *a*, thick cuticle; *b*, cell cavity. Note the thin cellulose walls, all round the cell cavity with the cuticle secreted over the outer surface. The shaded layer is probably a mixture of cutin and cellulose and the clear layer cutin alone.  $\times$  about 250.

### The Proteins

These are the most important of the nitrogen-containing substances in plants. They are on a different footing from the substances already described in two important ways. In the first place they always contain nitrogen and sulphur. Secondly, the carbohydrates and fats, though included within the living protoplasm, are non-living "metabolites," i.e. substances worked upon by the protoplasm itself. Some proteins fall into this class also, but others seem to be more intimately concerned with the make-up of the protoplasm itself. So far as we can understand this matter at present, it seems certain that some of the proteins are the very warp and woof of living matter.

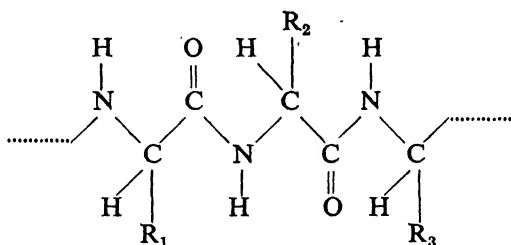
Chemically proteins are the most complex substances known. Chemists have not yet been able to work out the molecular structure of any single protein, far less to synthesise one. Edestin, which is probably one of the least complicated proteins, is said to have an empirical formula roughly as follows:



It is not surprising, therefore, that all the atoms have not yet been assigned to their proper spatial positions within the molecule, but

not until this has been done shall we understand its nature. Slight differences of molecular structure are sufficient to cause differences of behaviour between proteins, so that it is evident that enormous numbers of proteins showing varying degrees of distinctiveness are likely to exist. It is likely that such protein differences lie at the base of the differences between the protoplasts of different organisms.

Proteins may be regarded as being built up of *amino-acids* of which about twenty have been obtained from the proteins of plants. The simplest is *glycine*, or amino-acetic acid,  $\text{H}_2\text{N}.\text{CH}_2.\text{COOH}$ . The molecule of any amino-acid exists mainly as an internal salt or hybrid ion, e.g.  $^+\text{H}_3\text{N}.\text{CH}_2\text{COO}^-$ . As it carries with it at least one charge of each sign, it can react both with strong acids and strong alkalis, giving two series of salts, e.g. glycine hydrochloride and sodium glycinate. Two or more amino-acids may similarly combine to form a *peptide* and build up chain molecules of great length.



Polypeptide chains containing up to nineteen amino-acids have been synthesised artificially. They show some of the simpler protein reactions, but a molecule approaching the complexity of a true protein has never been formed artificially. The side chains  $\text{R}_1$ ,  $\text{R}_2$ ,  $\text{R}_3$  in the formula above differ according to the amino-acid concerned. They may include additional acid or basic groups and may even form cross-connections between parallel peptide chains in building up the complete protein molecule.

Proteins are precipitated from their solutions by the so-called "protein reagents" such as lead acetate, and trichloroacetic acid. They also give characteristic colour reactions such as the xanthoproteic ("yellow protein"), biuret and Millon's reactions (see Exp. (7), p. 84). A dilute solution of iodine precipitates proteins, at the same time staining them a bright and shiny yellow.

Different types of proteins are recognised according to their solubilities in different reagents.

*Albumins*: soluble in water and neutral salt solutions.

*Globulins*: insoluble in water but soluble in neutral salt solutions.

*Prolamins*: insoluble in water and salt solutions but soluble in dilute alcohol.

*Glutelins*: insoluble in all the above solutions but soluble in dilute acids and alkalis.

Albumins and globulins may exist as active substances in living cells; but the globulins may also accumulate to the point of precipitating out in more or less crystalline condition. They then form the *aleurone grains* found in the storage tissues of some seeds and sometimes in the resting embryos themselves.

Prolamins and glutelins, being insoluble under biological conditions, are usually found as reserve proteins in seeds (Fig. 38). The prolamins are limited to the grains of cereals—wheat, barley, etc.

Proteins are capable of combining with a wide range of other substances found in cells, many of which are probably held by these means on protein surfaces. Chlorophyll is combined as a chromoprotein and fatty materials form lipoproteins. Nucleoproteins include a complex phosphorus-containing substance, nucleic acid.

#### *Other Organic Substances*

There are, of course, many other classes of organic substances found in plant cells besides the three mentioned.

The so-called "aromatic substances" occur universally in plants. They contain carbon, hydrogen and oxygen and are founded on the structure known as the benzene ring. They include the tannins in bark and the pigments of flowers and autumn leaves. Numerous heterocyclic ring compounds, with nitrogen as well as carbon in the ring, occur also. They include alkaloids and simpler plant bases whose function as enzyme components, vitamins, hormones, etc., is becoming better understood. Plant acids are mentioned on p. 91.

#### *Enzymes*

The importance of enzymes lies in the fact that they act as catalysts to many of the chemical changes occurring in living protoplasm. A catalyst is a substance that accelerates a chemical change

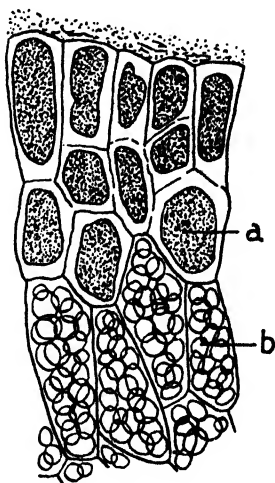


FIG. 38.—Cells from a barley grain. *a*, outer layer of aleurone cells with abundant reserve protein; *b*, inner cells with starch grains and little protein.  $\times$  about 250.

without itself becoming one of the products of the reaction, or otherwise altering the end achieved. In a reversible reaction it accelerates both components equally and does not alter the equilibrium, but only the speed with which it is achieved. The most important inorganic catalyst is the hydrogen ion ("acidity") but there is also a special type of catalyst whose action is due to the possession of an extensive surface to which the reacting substances may temporarily be attached. One of the best-known inorganic "surface cata-

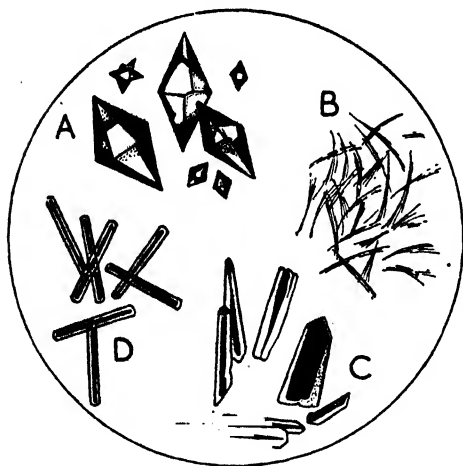


FIG. 39.—Crystalline enzymes. A, pepsin, a proteinase. B, lactic dehydrogenase. C, carboxypeptidase. D, trypsin, a proteinase. Various magnified. B, after Straub, the others after Northrop.

lysts" is powdered charcoal that has been recently heated. At one time it was supposed that the mere possession of a vast surface was the sole contribution of such a catalyst, but it is now apparent that there are spots of high activity in which the catalytic powers are localised. Powdered charcoal is said to have four different kinds of active centres and to carry out four different types of catalysis in consequence.

Enzymes are all proteins and some have been obtained in a good state

of purity (Fig. 39). As proteins they provide a good deal of colloidal surface (see p. 34) at which reaction can take place. Many enzymes, particularly those catalysing oxidations, need dialisable coenzymes or have prosthetic groups, which provide special reaction centres. Owing to their protein nature, enzymes are readily inactivated by heat, protein precipitants (see p. 80), and many special poisons; and they are highly specific. Unlike the hydrogen ion, a given enzyme can only catalyse one kind of reaction, e.g. hydrolyse starch or oxidise a particular organic acid, etc. A great variety of enzymes exists in every living cell; some fifty or more are well known, and the total number is doubtless much greater. They are mostly soluble in water and can usually be made to catalyse their reactions in solutions outside the living cell.

The enzymes mentioned later in this book and the reactions they catalyse are as follows. The termination *-ase* denotes an enzyme.

1. *Hydrolases*, hydrolysing and condensing enzymes.

Lipase, catalyses fats  $\rightleftharpoons$  fatty acids + glycerine.

Amylase, catalyses starch  $\rightarrow$  maltose.

Maltase, catalyses maltose  $\rightleftharpoons$  glucose.

Invertase, catalyses sucrose  $\rightarrow$  glucose + fructose.

Proteinases, catalyse proteins  $\rightleftharpoons$  polypeptides.

Polypeptidases, catalyse polypeptides  $\rightleftharpoons$  amino-acids.

2. *Phosphorylase*, catalyses starch +  $H_3PO_4 \rightleftharpoons$  glucose-1-phosphate.

3. *Desmolases*, enzymes splitting C-C linkage without hydrolysis.

Zymohehexase, catalyses hexosediphosphate  $\rightleftharpoons$  triosephosphate.

Carboxylase, catalyses pyruvic acid  $\rightarrow$  acetaldehyde +  $CO_2$ .

4. *Oxidoreductases*, oxidising and reducing enzymes.

Dehydrogenases, catalyse transfer of  $H_2$ .

Oxidases, catalyse transfer of  $H_2$  to  $O_2$ .

## Practical Work

### A. CARBOHYDRATES

(1) Compare the samples of solid glucose and solid sucrose provided. Note that the first is a crystalline powder, while the second forms large well-defined crystals. Compare their sweetness by tasting. Dissolve the samples in two separate test tubes each containing a little water and note that each dissolves completely. Test a little of each with a very dilute solution of iodine in potassium iodide,<sup>1</sup> and note that there is no change of colour. Add a few drops of Fehling's solution (7 per cent. copper sulphate made strongly alkaline by mixing immediately before use with an equal quantity of 35 per cent. sodium potassium tartrate + 10 per cent. caustic soda) to each test tube and heat. Note that one solution turns red, owing to the precipitation of red cuprous oxide, while the other does not.

(2) Hydrolyse a sucrose solution by adding a few drops of strong sulphuric acid and boiling for 5–10 minutes. Neutralise to litmus with caustic soda and then apply Fehling's test.

(3) Examine a thin slice of potato under the low and high powers of the microscope. Draw one or two of the starch grains under the high power. Irrigate the section with very dilute iodine solution by placing a drop to one side of the coverslip and applying blotting paper to the other, then examine again.

(4) Examine under the microscope a cotton hair teased out of a piece of cotton-wool. Apply a drop of Schulze's solution (chlor-zinc-iodine) and observe again. Note both the blue coloration and the great swelling of the cellulose.

(5) The solution in the demonstration flask has been produced by boiling a good quality writing paper (cellulose) for a long time in water containing 10 per cent. sulphuric acid. Neutralise a few ml. in a test tube with strong caustic soda and then test with Fehling's solution for the presence of reducing sugar (glucose).

<sup>1</sup> In future this solution will be referred to as iodine solution and iodine in alcohol as tincture of iodine.

Examine similarly the solution prepared by the same method from date-stones whose very thick cell walls consist mainly of **hemicellulose**.

#### B. FATS

(6) Note that the desiccated coconut "meat" (food material consumed by the embryo growing into a seedling) is oily to the touch. Place some in a test tube with water and boil; the oil rises to the surface. Add a few drops of Sudan III (an aniline dye) and allow to stand. The oil is coloured red. Similar observations may be made with crushed linseed or castor-oil beans.

Add a few drops of Sudan III to olive (or linseed) oil in a test tube; the oil is coloured red. Pour half the red oil into another test tube. Add a little alcohol to one and water to the other. Note the position taken up by the alcohol and water respectively in relation to the oil; also the coloration resulting. Note the effect (and endeavour to explain it) when a drop of oil is placed on paper.

#### C. PROTEINS

(7) The two substances provided in separate test tubes are (a) white of egg (an **albumin**) shaken up with water, and (b) bean meal (a **globulin**) shaken up with salt solution. Divide each into six portions and test as follows:

- (i) Add a little lead acetate solution; the protein forms a white precipitate.
- (ii) Add a little 10 per cent. trichloroacetic acid solution; there is a white precipitate.
- (iii) Add a little iodine solution; there is a yellow precipitate.
- (iv) Add a few drops strong nitric acid. Boil and then cool thoroughly. There is a yellow coloration of the protein. Make alkaline with ammonia solution; the yellow colour changes to orange (xanthoproteic reaction).
- (v) Add *one drop* of dilute copper sulphate solution. Now add excess of caustic soda or potash. A purple colour, or ring, where the solutions meet is given by the protein (Biuret reaction).
- (vi) Boil with Millon's reagent. The protein gives a brick-red precipitate.

#### D. ENZYMES

(8) The tube provided contains dilute starch paste. Pour a little into a watch-glass and add one drop of very dilute iodine solution. Now add 1 per cent. **taka-diastase** (a commercial preparation of *amylase* also containing *maltase*) to the contents of the tube and shake the tube vigorously. After a minute, pipette a little of the mixture into another watchglass and add a drop of very dilute iodine. Shake the tube again and after another two minutes pipette a further sample into a third watchglass and test as before. Continue until a colour is no longer given on adding iodine. The purple colour given with iodine is due to the formation of dextrins (see p. 77). After about half an hour add Fehling's solution to the residual contents of the tube and test for the presence of reducing sugars.

## Chapter VII

# PLANT METABOLISM<sup>1</sup>: RESPIRATION<sup>2</sup>

### METABOLISM

Synthesis in plant cells does not come to an end with the formation of sugars; indeed this may in a sense be regarded as a beginning. All living things need *organic food* to support their growth and maintenance. The three great classes of food substances are the carbohydrates, fats and proteins described in the last chapter. Animals and the heterotrophic plants (p. 362) must absorb these from their surroundings. They change and modify them into the varied materials of their own bodies; but the substances with which they begin are already complex organic compounds, rich in energy capable of being transformed (cf. p. 92). The green plant alone is capable of absorbing simple inorganic materials, such as carbon dioxide and salts found in the soil, and of building them up into organic foods. In this sense the green plant may be said to manufacture its own food; *food* being defined as *a substance from which an organism derives transformable energy and material for maintenance and growth*. Carbon dioxide and soil salts do not provide a plant with energy, and are therefore not plant foods according to this definition; they are often called the raw materials of plant food, but sometimes also plant nutrients.

### *Synthesis and Anabolism<sup>2</sup>*

The primary plant foods are sugars and from the sugars of photosynthesis all other plant foods, body substances and protoplasm itself are built up. The number and variety of such syntheses known to occur in green plants is very great and exceeds those occurring in heterotrophic plants and animals or in the laboratory of the organic chemist. Cotton, wood, the vitamins, oils, rubber, spices, many drugs, resins, perfumes, fibres, gums, tannins and the colours of flowers are a few of their products. All these syntheses are collectively referred

<sup>1</sup> Greek μεταβολή (metabole), change.

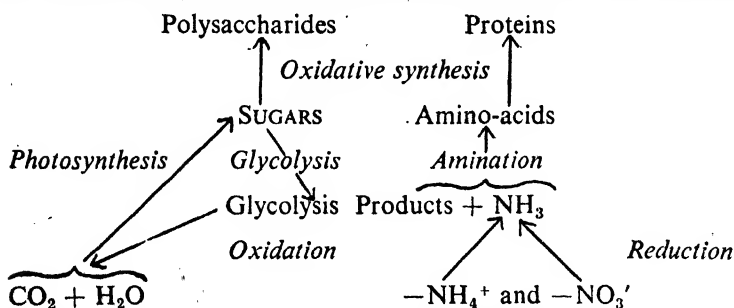
<sup>2</sup> Greek prefix ἀνα- (ana-), up or anew.



to as *anabolism*. The significance of many of them in the life of the plant is still far from clear; but others are of obvious importance.

**Carbohydrates.** The body substances of plants are built mainly of carbohydrates and their derivatives. Cell walls form a large proportion of the solid material of an adult plant. They consist of cellulose formed by successive condensations of glucose (p. 77), and of modifications of cellulose such as *lignin*, the material of woody cell walls. Other carbohydrates forming part of the permanent plant structure are the *pectic substances* of the middle lamella, and mucilages, such as the agar formed over the surface of some of the red seaweeds. All these are synthesised by anabolism and are of definite significance in the lives of the plants forming them.

**Proteins.** Proteins are the basic constituent of protoplasm and of the enzymes it contains. They are built up from sugars and from nitrogenous substances obtained from the soil, viz. nitrates and ammonium salts. Protein formation involves many stages. It occurs in both roots and leaves and may be brought about by different methods. It is limited to young and active tissues and is specially active in meristems. Nitrate,  $-\text{NO}_3$ , must first be reduced to ammonia,  $\text{NH}_3$ . The ammonia does not react with sugars, however, but with simpler substances formed by glycolysis.<sup>1</sup> This interaction produces amino-acids (p. 80) which condense in determinate patterns to form the proteins. An important new effect comes in here, namely that, during their working up to more complex substances, the sugars may be remodelled to more reactive substances by partial breakdown. Metabolism is a vast complex of interlocking reactions which cannot really be



separated into neat compartments, though we may attempt to recognise divisions to help us through the maze. Some of the more obvious and important directions of reaction are summarised above.

<sup>1</sup> Sugar breakdown, from Greek  $\gamma\lambda\upsilon\kappa\acute{\upsilon}\varsigma$  (glucous), sweet and  $\lambda\acute{\upsilon}\sigma\iota\varsigma$  (luis), loosing or setting free.

*Plastic Substances. Reserves and Intermediates.* Besides the body-forming *end-products* of metabolism, other substances may accumulate in considerable quantities and disappear again afterwards. These are called *reserve substances* and outstanding examples are starch and the fats. In the higher plants starch is a typical reserve in the vegetable organs and fats in the storage tissues of seeds. Still another class of substances may be difficult to detect because they are present only in small amounts or mere traces. These usually have the nature of *intermediate products*.

The relation between these various classes is most easily understood by considering the relative rates of the reactions that form or destroy the substances concerned. Thus the fact that starch is formed in leaves by day and disappears at night is mainly due to the relative rates of formation and breakdown. Formation ceases by night owing to the cessation of photosynthesis, whereas the hydrolysis of starch goes on at all times, day and night alike.

Consider also a series of reactions such as the stages of protein formation mentioned above.

Glycolysis products + ammonia  $\rightarrow$  amino-acids  $\rightarrow$  proteins.

(1) (2)

If (1) is a relatively slow reaction and (2) faster, then the amount of amino-acid present will necessarily be very small. If the difference of rate is considerable, the concentration of amino-acid may be reduced to vanishing point. For this reason it may often be impossible to detect analytically the presence of substances that we have reason to believe should exist as intermediate products. They should, however, appear if we can specifically inactivate or poison the enzyme responsible for their removal. This method of the "enzyme block" has played a great part in the elucidation of intermediate metabolism. For example, the poisoning of carboxylase (p. 83) with 1-naphthol-2-sulphonic acid causes pyruvic acid to appear in metabolising leaves.

The extent to which substances accumulate in protoplasm with its complex constitution is unlikely to be the same as in a simple solution of the reactants concerned. We must not hastily conclude that the plant may therefore be said to be laying up "reserves" for some specific purpose, such as nourishing the young embryo in the seed or maintaining itself during the night. Their accumulation is a direct outcome of the chemical and physical properties of the protoplasm and its inclusions. Any "use" they may be to the plant is a result of their formation, not its cause.

### *Digestion*

Plant foods accumulate in seeds, tubers and other storage organs (Fig. 34) which often—though by no means always—pass through a period of dormancy. When activity begins again the insoluble reserve substances are broken down by enzymes to simpler soluble products. Thus in spring the starch of potato tubers is mobilised as a mixture of sugars by amylase and associated enzymes and the sugars pass into the young sprouts. The oils in many seeds are hydrolysed to fatty acids and glycerol by lipases (p. 78) and the reserve proteins to amino-acids and amides. This enzymatic returning of substances to metabolic circulation is called digestion and is analogous to the similar process that goes on in the gut of an animal after taking solid food, or in the food vacuole of *Amæba* (p. 19).

### RESPIRATION<sup>1</sup>

It has long been known that plants, like all other organisms, continuously absorb oxygen and give off carbon dioxide. This goes on in green cells as well as all others, but is commonly masked by the converse gas exchange of their photosynthesis.

Under conditions favourable for photosynthesis this is usually 5–10 times faster than the respiratory exchange; but in the absence of light the respiration of green cells may be readily demonstrated also. The term respiration is no longer—as it was originally—synonymous with breathing. Only animals breathe, i.e. have special organs, lungs and gills, for the intake of air containing oxygen into the body and the expulsion of air enriched with carbon dioxide. Plants are entirely passive in this respect; oxygen and carbon dioxide diffuse into and out of the plant body along the intercellular spaces (p. 44) by virtue of their own molecular movements.

The absorption of oxygen and release of carbon dioxide are significant because they are the index of important changes continually going on inside the living tissues and in some way necessary to their existence. These internal events are all included under the heading of plant respiration. They include a wide range of reactions all occurring under the influence of the living protoplasm and its enzymes. For simplicity we may regard respiration as beginning with the sugars, the same glucose, fructose and sucrose mixture that is formed after photosynthesis, and ending with their degradation to carbon dioxide or some partially oxidised product such as alcohol or a plant acid. Healthy plant tissues, unlike those of animals, do

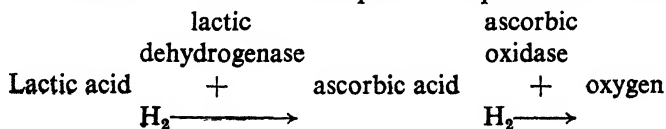
<sup>1</sup> Latin *respiratio*, taking a breath.

not normally respire proteins to compounds such as urea, or release free ammonia. Although considerable changes among the plant's complex nitrogenous compounds are always going on, these are more conveniently classified as a nitrogen metabolism whose relations to respiration will become clearer as we go on.

### *Aerobic Respiration*

Normal respiration in air has two types of initial reactant, the sugars produced by photosynthesis and the air's oxygen. This does not mean that sugar and oxygen themselves interact even inside living cells. This is, in fact, now known to be extremely unlikely and respiration consists, just like photosynthesis, of a long series of reaction stages. Its course is determined not only by enzymes but also by the phosphate ion  $\text{—H}_2\text{PO}_4'$  which forms intermediate compounds and so acts as a catalyst within the protoplasm. Even inside protoplasm the sugars are apparently stable substances and the first step in respiration is not an actual break-up of the sugar molecule but the formation of a phosphate ester, *hexosediphosphate*. This is decomposed by the enzyme *zymohexase* followed by others, so that a variety of glycolysis products is formed. So far the events are independent of oxygen and will occur in plant tissues temporarily deprived of it. Plant respiration, in fact, includes two main types of change which may be termed glycolysis and oxidation respectively. Each involves numerous reactions.

*Plant Oxidations.* The great majority of biological oxidations are of the type that involves the transfer of hydrogen from the substance oxidised to the substance reduced. In respiration, hydrogen is transferred from products of glycolysis to the oxygen of the air. There is no direct interaction between the first substance to lose hydrogen and the oxygen; indeed, quite a considerable number of shifts may take place by way of intermediate *hydrogen carriers* before the hydrogen finally reduces the oxygen to water. Each step is catalysed by its appropriate enzyme, called from its function a *dehydrogenase* (p. 83). The enzyme which finally transfers the hydrogen to atmospheric oxygen is called a terminal *oxidase*. The respiratory oxidations are not necessarily identical in all plants. An example of a short oxidation sequence which is believed to occur in some plants is represented as follows:

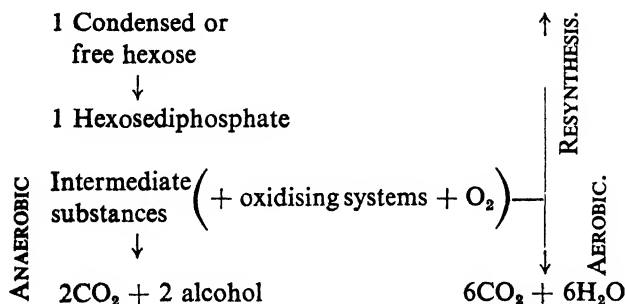


Ascorbic acid is a carrier, or "redox body," being itself alternately oxidised and reduced. Lactic acid,  $\text{CH}_3\text{CHOH COOH}$ , is oxidised by loss of hydrogen to pyruvic acid,  $\text{CH}_3\text{CO COOH}$ , and the oxygen is reduced to water.

### *Anaerobic Respiration*

When plants are deprived of oxygen, or their terminal oxidases are put out of action with minute doses of cyanide, they continue to give off carbon dioxide even though no oxygen is taken up. This anaerobic respiration may continue for a while, but the cell mechanism breaks down if it goes on for long. In anaerobic respiration, glycolysis, i.e. the phosphorylation of sugars and the breakdown of the sugar-phosphate ester, continues; but the normal oxidation stage is obviously ruled out. In the absence of oxygen to act as hydrogen acceptor, some of the glycolysis products, notably acetaldehyde, fulfil this role and are in consequence reduced. Acetaldehyde is thus reduced to alcohol which accumulates in the anaerobically respiring cells and, being a poisonous substance, is one of the causes of cellular breakdown in the absence of oxygen. The glycolysis products which lose the hydrogen are by successive stages converted to the carbon dioxide which continues to come off. Although fewer molecules of carbon dioxide are derived from one hexose molecule in anaerobic than in aerobic respiration, the rate of sugar breakdown is often accelerated to such an extent that for a time carbon dioxide is released faster under nitrogen than in air.

The relations between aerobic and anaerobic respiration are summarised as follows:



There are considerable similarities between the anaerobic respiration of plants in general and the alcoholic fermentation of sugars by yeast (p. 342). Anaerobic respiration is, however, usually extinguished,

at concentrations of oxygen above 5 per cent., whereas yeast carries on its fermentation even in normal air with 21 per cent. oxygen.

### *Respiration of Succulent Plants*

Plants with very thick fleshy leaves or stems often release only small amounts of carbon dioxide in the course of their respiration. During the aerobic respiration of ordinary plants about one molecule of carbon dioxide is released for every molecule of oxygen consumed. The respiratory quotient  $\text{CO}_2/\text{O}_2 = 1$ . In succulent tissues the ratio may fall as low as 1/10. Oxidation of sugar products in these tissues is incomplete and does not proceed as far as complete conversion to carbon dioxide, even though the tissues may be permeated by oxygen from the air. Their enzyme equipment may perhaps differ from that of normal plants. Instead of carbon dioxide they form plant acids such as malic acid and iso-citric acid which accumulate in the tissues to an extent which gives them a sharp taste. The tartness of unripe fruits and sorrel leaves is due to the same cause. The mould fungi (p. 363) show a similar tendency towards the formation of acids. The ratio of oxygen to carbon is higher in these acids than in sugars, but lower than in carbon dioxide. Both glycolysis and oxidation probably take place during their formation, though the oxidation is less complete than in normal types of respiration. During periods of illumination the acids are consumed and disappear again. They may be built back to carbohydrates or other body substances, but evidence is still scanty.

### *Respiration of Fat-storing Tissues*

It has often been observed that the respiratory quotient of fat-containing tissues such as seeds and algal spores is lower than the usual value of 1 which occurs when sugars or starch are being consumed. Fats have a lower ratio of oxygen to carbon in their molecules than carbohydrates, so that their complete oxidation to carbon dioxide involves a greater consumption of oxygen for each molecule of carbon dioxide produced. The exact value of the  $\text{CO}_2/\text{O}_2$  ratio depends on the particular fat or mixture of fats oxidised, but does not vary much from 0.7. In tissues that are consuming fats, two stages may be recognised, (a) digestion of fats to sugars, and (b) respiration of sugars to carbon dioxide. If the two stages are proceeding at a uniform rate, a  $\text{CO}_2/\text{O}_2$  quotient approximating to 0.7 is likely to be found. If the first reaction is going on faster than the second, even lower values will result because the conversion of fats

to sugars consumes oxygen without the production of any carbon dioxide. Values as low as 0.3 are observed for a short time during the germination of fatty seeds, and sugars and starch accumulate simultaneously.

### *Energy Changes During Respiration*

Energy is transformed during both aerobic and anaerobic respiration, but most abundantly during the oxidation stages of the latter. The breakdown of 1 gram-molecule of hexose "liberates" about 72 k.cals. of free energy if carried out anaerobically, and 710 k.cals. or nearly ten times as much, aerobically. Animals devote a great deal of their energy so produced to doing mechanical (muscular) work; but only the minutest amounts of work are done by plants. In a plant that has stopped growing the respiratory energy is all converted to heat and dissipated into the atmosphere. In this it resembles the carbon dioxide escaping at the same time, but both the carbon dioxide and the energy may have passed through interesting and important changes inside the plant before being released. It is usual to say that this continual energy turnover sustains the living condition of the protoplasm, but precisely what this means is not at all clear.

A spontaneous reaction that proceeds with a decrease of free energy (i.e. energy able to do work) "releases" energy; but a reaction which involves an increase of free energy "needs" energy, and will only happen if it is somehow provided. Many of the reactions described under the heading of synthesis and anabolism (p. 85) are of the latter kind. Proteins, for example, can only be formed from sugars and nitrates if energy is provided. Even some of the reactions of respiration itself, such as forming esters, need a little energy, but others, particularly the oxidation stages, release a lot more. Provided that the complete series shows a net "release" of energy (= decrease of free energy) which, of course, respiration does, the reaction series as a whole can go forward. Syntheses must be chemically linked to oxidations to enable them to occur and it is found that, although a plant may survive and respire anaerobically, all growth and synthesis comes to a stop. The nature of the chemical mechanism linking any one synthesis to the respiratory oxidations is still unknown.

Absence of oxygen also stops cell division, circulation of the protoplasm, germination and absorption of salts into roots as well as synthesis. It is therefore clear that although respiration may at first sight appear to be destructive, its principal significance is con-

structive. It carries on the work of building up the plant body from the simple sugars provided by photosynthesis and the inorganic nutrients absorbed from the soil. At the expense of breaking down some of the sugar molecules formed, others are further elaborated into the immense variety of substances and structures that compose the living organism.

### *Respiration in Plants and Animals*

Respiration serves the same constructive ends in animals as in plants. It is, indeed, similar in its fundamentals in all organisms whether simple or complex, plant or animal. Even the means by which it is achieved, i.e. its various chemical reagents and stages, show considerable similarities in such widely different organisms as the higher animals and the higher plants. Hexose units are in both the commonest materials consumed and both may use fats as well as polysaccharides to supply them. Phosphates have a very wide distribution in both kingdoms as catalysts of sugar breakdown, and the glycolysis products are similar. Pyruvic acid, for example, is probably commonly found in both. There are, of course, minor differences such as the more ready consumption of a proportion of proteins in animal tissues and their formation of lactic acid rather than of alcohol under anaerobic conditions. But plant (or animal) tissues may differ among themselves more than this. We may perhaps best think of respiration as a fundamental process which different organisms carry out in slightly different ways. Its necessity and the general method of attaining its end are inescapable attributes of life as it exists.

## Practical Work

### METABOLISM

(1) Some characteristic products of plant metabolism may be identified by the following methods.

(a) *Starch*. Examine a thin slice of potato under the low and high powers of the microscope. Draw one or two cells with their included starch grains. Irrigate the section with a little *very dilute* iodine solution by placing a drop to one side of the coverslip and applying blotting or filter paper to the other. Note the blue coloration characteristic of starch and the eccentric hilum, origin of the grain, and the successive rings of starch deposition.

(b) *Cellulose*. See Exp. (4), p. 83. Cut a thin section of any young stem and treat similarly with chlor-zinc-iodine. Note the reaction of the cellulose walls, especially in the outer tissues.

(c) *Cutin*. Cut a transverse section of any thick leaf such as cherry laurel. Treat with chlor-zinc-iodine. Carefully observe the outer wall of the epidermis.



It will show an inner blue layer of cellulose and a shining yellow outer layer of cutin.

(d) *Lignin*. Cut a thin section of a match stalk or woody twig. Treat with aniline sulphate or with phloroglucinol followed by a drop of strong hydrochloric acid. Observe under the microscope the lignified walls stained yellow with aniline or red with phloroglucinol.

(e) *Protein*. Mount a young root tip from a sprouting barley grain in a drop of Millon's reagent. Cover with a slip and warm gently. Observe through the microscope the red coloration of the abundant proteins in the meristematic cells.

(f) *Alkaloids*. Mount the tip of a very young barley root from a grain just starting to sprout in a drop of water. Irrigate with very dilute iodine and watch carefully. As the iodine enters, the cell proteins colour a shining yellow and a brick-red precipitate is thrown down in the vacuoles of the cells just behind the meristem. This is *hordenine*, an alkaloid which gives the medicinal value to barley water. Alkaloids are complex nitrogen compounds found in the vacuoles of many plant cells.

(g) *Tannin*. Boil some shavings of the outer bark of horse chestnut, walnut or larch with a little water. Strain off the extract and add one drop of 5 per cent. ferric chloride solution. A green coloration reveals the presence of tannins.

#### DIGESTION

(2) Examine grains of barley that have been germinating for 1, 2, 3 . . . days up to a week. Note how the reserve tissue becomes first soft and then milky owing to the breakdown of the cells. Tease out a little of the reserve tissue at each stage, mount and examine under the microscope. Irrigate with a little very dilute iodine. Note the progressive corrosion of the starch grains as they are broken down by enzymes inside a resistant outer pellicle which is only penetrated here and there.

NOTE.—The action of the starch hydrolysing enzymes is examined in Exp. (8), p. 84.

#### RESPIRATION

(3) About half fill a test tube with actively sprouting barley grains or peas. Cork securely and keep in a warm place overnight. Take a pipette or piece of glass tubing about 5 mm. diameter and draw limewater into its lower end. Open the test tube and quickly insert the lime-water tube so that its tip is just above, but not actually touching, the seeds. A white cloudiness in the lime-water will denote the *formation of carbon dioxide*.

(4) Fill and incubate a second test tube as above. Open and insert immediately a glowing splint. It will be extinguished at once owing to the *consumption of oxygen* in the tube by the respiring seeds.

(5) Fill a thermos flask to about two-thirds of its capacity with germinating seeds, and a second flask with seeds that have been killed by boiling. Insert a long-stemmed thermometer into each so that the bulb is well buried among the seeds. Close the neck of each flask with a tight wad of cotton wool and observe the temperatures from time to time. The *liberation of heat* from the living seeds will cause the temperature to rise in the enclosed system. Normally the heat would dissipate and no appreciable rise would be perceptible round the respiring tissue.

## Chapter VIII

### THE GREEN ALGÆ ORIGIN OF SEX AND OF THE SOMA

Life probably began in the sea, and some at least of the earliest organisms are likely to have been minute free-floating forms which were able to absorb and use light energy to build up their bodies from simple inorganic substances, and which would therefore be classed as plants. Of these some developed flagella and became actively free-swimming, and their descendants are still represented by unicellular plants living in the sea or in fresh water. All these free-floating and free-swimming organisms, whether animals or plants, are collectively called Plankton.<sup>1</sup> The earliest stages of the evolution of complex organisms involve the grouping together of two or more such cells, and this may occur in a number of ways. The large group of simple plants called the Algæ<sup>2</sup> shows immense diversity of form and about 17,000 species have been described, ranging from the microscopic, such as *Protococcus*, to the immense kelps of the Pacific coasts that may be 50 metres long (cf. p. 124). The multicellular species exhibit great variety in the ways in which their cells are related to one another. They may be regarded as the still living descendants of early plants that reached only a limited degree of specialisation and complexity. Many of these forms proved to be "experimental" in the sense that they could not lead on by further evolution to yet more highly differentiated and efficient plants. *Volvox* and *Spirogyra*, described later in this chapter, are examples of organisms of this kind. In other algæ, such as the brown seaweed *Fucus* (Chapter IX), quite a large bulky plant, we see a foreshadowing as it were of the complex structure of a highly evolved land plant, and the possibility of a further evolution leading on step by step to this end. The following are some of the more important methods of aggregation still recognisable in living algæ.

1. THE FILAMENT. This is formed by attachment of the cells end

<sup>1</sup> Greek πλαγκτός (plagktos), wandering.

<sup>2</sup> Latin, seaweed.

96 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA to end in a long thread, i.e. in one dimension only. It may be free-floating with no further modification of the cells, e.g. *Spirogyra* (p. 115). The filament may, on the other hand, develop branches (e.g. *Stigeoclonium*), and growth may be limited to an end cell. One end cell may become specialised for attachment as in *Ulothrix* (p. 113); but this is the limit of differentiation that can occur in a simple filament.

2. **FLAT PLATE.** This is formed if the individual cells become linked up in a single plane only, but in two dimensions. It is seen in

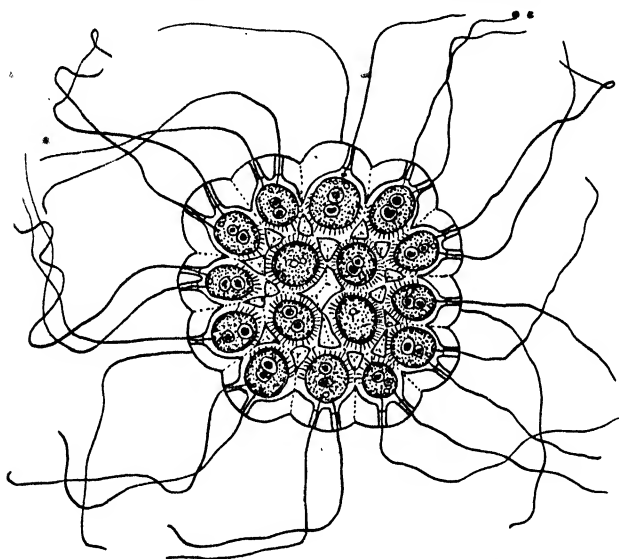


FIG. 40.—*Gonium pectorale*. Cœnobium of 16 cells embedded in a flat plate of mucilage from which the flagella protrude.  $\times$  about 600. After Belar.

the curious little alga, *Gonium* (Fig. 40), found in some freshwater ponds. The limits of mechanical stability of this arrangement are soon reached since the cells and their materials are composed of soft sols and gels. *Gonium* itself is very readily broken up into separate cells by rough treatment like centrifuging.

3. **HOLLOW SPHERE.** This is a simple arrangement of cells in three dimensions of space with all the cells in a single layer at the surface. It attains its highest development in *Volvox* (p. 108) and is stable to a larger diameter than the flat plate, but reaches its maximum near the lower limit of what can be seen directly by the naked eye.

4. **SOLID MASS,** with inner and outer cells. This possesses numerous possibilities of further development and differentiation and

enables the plant to grow very much larger. Nearly all organisms visible to the naked eye may be said to have developed along this line of cellular aggregation. Of the very numerous algæ belonging to this class *Fucus* will be described as an example (p. 124).

### “Immortality” of Unicellular Organisms

The body of a unicellular form—such as an amœba, a bacterium or a yeast plant—not only feeds and grows, it also divides and produces new individuals of the species. This production of new individuals, or *reproduction*, is in origin simply an extension of the growth process; it is *discontinuous growth* because it is growth conditioned by the separation of a part or parts of the individual to form new individuals. The protoplasm of the individual organism continues to exist and to increase in bulk, but it can only increase beyond a certain limit of size if it separates to form two or more new individuals. Under favourable conditions of life this process continues indefinitely, so that the protoplasm of which the organism is composed is immortal in the sense that it need never die so long as the conditions remain favourable to its continued life, though it dies of course as soon as the conditions become sufficiently unfavourable. But in the higher organisms—in the great majority of multicellular animals and plants—the functions of nutrition and growth are, as we know very well, separated from the function of reproduction. The feeding and growing body does in most cases regularly die after a certain time whether the general conditions of life continue favourable or not. It dies, as we say, of old age: it is a *soma*<sup>1</sup> or “mortal” body. On the other hand, the reproductive cells (germ cells) which it bears grow, under certain conditions, into new individuals of the species.

One series of green flagellated algæ, the “hollow sphere” series, beginning in *Chlamydomonas*<sup>2</sup> and culminating in *Volvox*, illustrates very beautifully the way in which the differentiation of sex among conjugating cells came into existence. The series also illustrates the origin of the soma, that is the body of the organism as opposed to its germ cells.

## CHLAMYDOMONAS

### Structure

The organisms belonging to this genus are very common in pools and rain-water tanks. Each is a minute green cell (Fig. 41 A); oval or

<sup>1</sup> Greek *σῶμα* (*sōma*), the body.

<sup>2</sup> Greek *χλαμύς* (*chlamys*), cloak, presumably referring to the cellulose wall, and *μονάς* (*monas*), a unit.

98 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
 sometimes rather oblong in shape, with a basin-shaped chloroplast occupying the hinder end of the cell and containing usually one

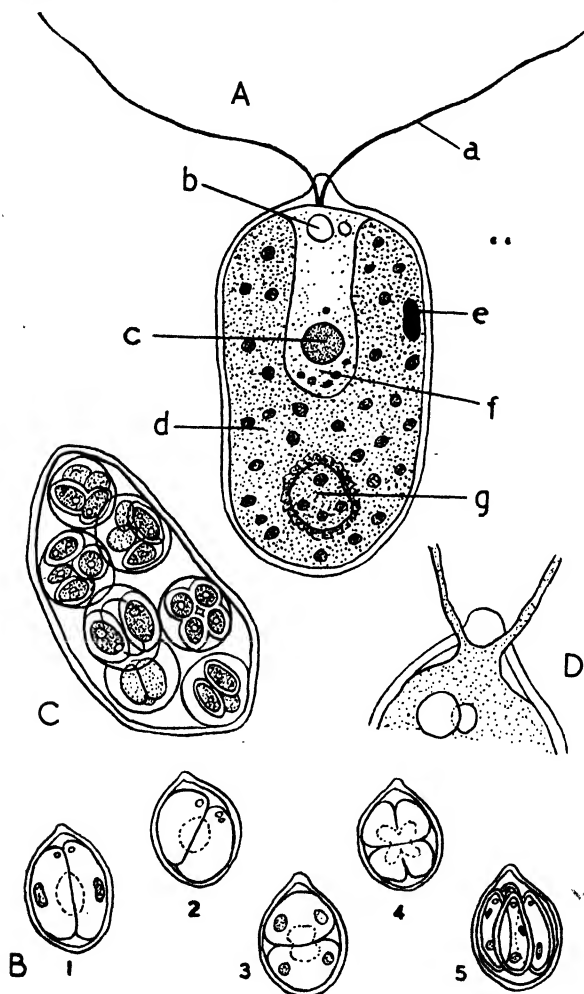


FIG. 41.—*Chlamydomonas*. A, a cell showing *a*, flagella; *b*, contractile vacuole; *c*, nucleus; *d*, chloroplast; *e*, eye-spot; *f*, central colourless cytoplasm; *g*, pyrenoid. B, stages of cell division. C, palmella-stage, after Goroschankin. D, anterior end of cell showing connection of flagella with the cytoplasm and passage through the cell wall. A, B and D after Diel. Highly magnified.

conspicuous pyrenoid. The chloroplast surrounds a central body of colourless cytoplasm containing the spherical nucleus. The front end of the cell also consists of colourless cytoplasm to which are attached

two delicate flagella of equal length; basal granules (p. 23) can be demonstrated at their point of connection with the cytoplasm by suitable staining. *Chlamydomonas* moves about actively with a rhythmical beating of the flagella, continually rotating on its long axis as it goes. The movement is similar in its speed and probably in its mechanism to the flagellate movement of *Euglena* (p. 23). The protoplasm of the cell is closely covered with a cellulose cell-wall thickened over the front end. The flagella pass through the wall in fine canals (Fig. 41 D). In some species the wall is thickened over the entire cell and is gelatinous. This thickening is very conspicuous in the allied genus *Sphaerella*, or *Hamatococcus* (Fig. 42), in which the soft gelatinous inner part of the wall is freely penetrated by protoplasmic fibrils which reach to the firmer outer layer.

*Chlamydomonas* possesses a red eye-spot or stigma (Fig. 41 Ae) which is situated in the surface of the protoplasm at the anterior end, somewhat to the side and near the attachment of the flagella. It consists of a biconvex hyaline lens (Fig. 43 Aa) in front of a curved plate carrying the pigment (Fig. 43 Ab). It is believed to be the site at which light stimulus is effective, and to be concerned with the regulation of the movement of the

flagella. It is noteworthy that eye-spots are commonly found in flagellated motile cells such as *Euglena*, *Chlamydomonas*, the zoospores of *Ulothrix* (p. 114) and similar Protista lacking chlorophyll, whereas non-motile cells such as *Protococcus* are without them. Another characteristic of free-swimming fresh-water cells possessed by *Chlamydomonas* is provided by two rather small contractile vacuoles also situated just behind the insertion of the flagella.

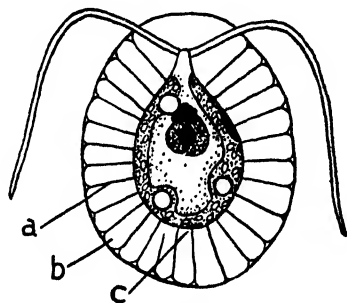


FIG. 42.—*Sphaerella lacustris*. a, protoplasmic fibrils; b, firm outer wall; c, inner gelatinous wall. After Reichenow.

### Nutrition

The nutrition of *Chlamydomonas* may be holophytic, i.e. it absorbs nutrient inorganic salts all over its surface from the water in which it swims. Through the agency of its pigmented chloroplast it is able to make sugars from dissolved carbon dioxide. The sugars may be further converted to starch which accumulates as grains or plates

100 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
 round the pyrenoid, itself a protein structure. In these respects *Chlamydomonas* behaves as a typical green plant; but it is noticeable that it thrives particularly well in water rich in decaying organic matter, such as farmyard pools. Many, at least, of its species appear to be saprophytic, so that in its nutrition *Chlamydomonas* most closely resembles *Euglena* (p. 26).

### Reproduction

**Asexual.** This is the commonest method in *Chlamydomonas*. Usually the cell comes to rest at the beginning of the process and the flagella are cast off or withdrawn. A few species remain motile during division. The protoplast divides longitudinally into two halves (Fig. 41 B1). It may then rotate within the cell wall, so that the division

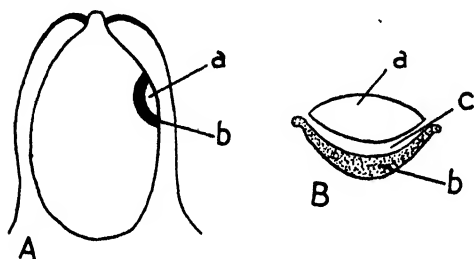


FIG. 43.—A, diagram of *Chlamydomonas* cell showing eye-spot; a, hyaline lens; b, plate of pigment. B, cross section through the eye-spot of *Volvox*; a, lens; b, pigment; c, photosensitive substance. After Mast.

between the daughter cells lies across the short diameter of the parent wall (Fig. 41 B2-3). The first division is followed by simultaneous division of the two daughter cells to four and, if conditions of growth prior to reproduction were good, a further division to eight may occur. The daughter cells each secrete a new cell wall and develop their flagella. They are finally released by the bursting or gelatinisation of the parent wall. Under favourable conditions, division takes place daily, usually towards evening, and is complete in a few hours. The daughter cells, even when they are the product of threefold division to eight, soon grow to the full size, usually 10–20  $\mu$ . Sometimes the daughter cells fail to develop flagella and remain embedded in the old cell wall which becomes mucilaginous and swells up greatly (Fig. 41 C). The mass is called a *Palmella*-stage because it resembles the alga *Palmella*, and may increase to a relatively large size by repeated division of the cells within the mucilage. It may finally break up by the cells forming delayed flagella and swimming away. *Chlamydomonas* may survive periods of partial desiccation in a *Palmella*-stage. It can survive even severer drying up as single resting spores in which the

protoplasm is withdrawn from the original wall and additional walls laid down inside. Such resting spores often develop a strong red coloration.

*Sexual Reproduction. Formation of Gametes.* Cell division sometimes continues beyond the eight-fold stage and as many as sixty-four daughter cells may be produced from a single parent, their size varying inversely as the number produced. In some species they

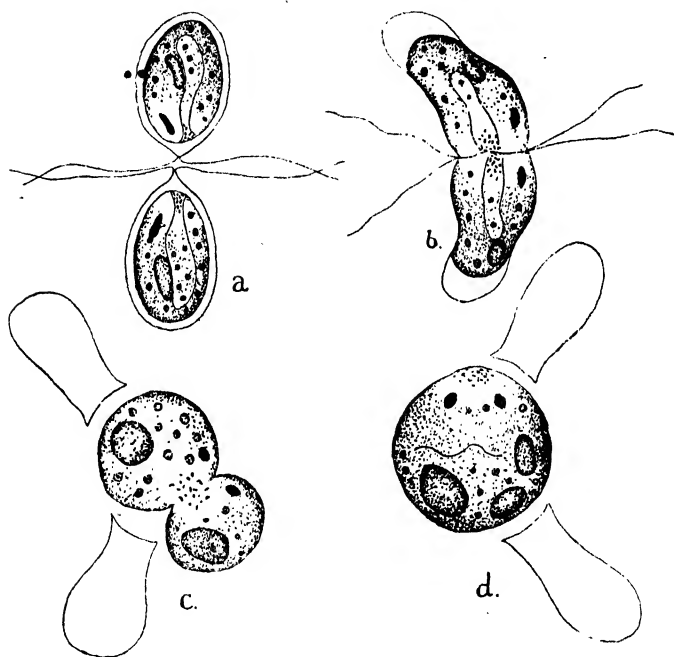


FIG. 44.—Conjugation of *Chlamydomonas*. *a*, approach of gametes; *b-d*, stages of fusion. After Diel.

secrete cell walls, in some their protoplasts are naked, though in other respects similar to the ordinary individuals. When these small and more numerous daughter cells are formed they do not, as a rule, grow directly into full-sized individuals, but conjugate in pairs and are therefore called *gametes*.<sup>1</sup> When two gametes come into contact at their front ends, their bodies gradually fuse completely (Fig. 44). If the gametes have cell walls the protoplasts slip out of them leaving the empty shells behind (Fig. 44 *c*). The single cell formed by the union of the two gametes is called the *zygote*.<sup>2</sup> It may continue to

<sup>1</sup> Greek γαμέω (*gameō*), marry.

<sup>2</sup> Greek ζυγώω (*zugoō*), yoke.



102 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA swim for a time with its four flagella, but finally settles down, becomes spherical and develops a thick, sculptured wall and conspicuous red pigment. It contains fats and reserve materials instead of starch like the normal vegetative cell. A similar occurrence of fat as the characteristic storage product of reproductive bodies is common throughout the plant kingdom (cf. *Spirogyra*, p. 118).

The zygote, like the spore, forms a resistant stage able to withstand unfavourable conditions. Its nucleus undergoes a reduction division (p. 148) and four daughter cells are produced. They develop flagella and, upon rupture of the zygote wall, become free-swimming individuals.

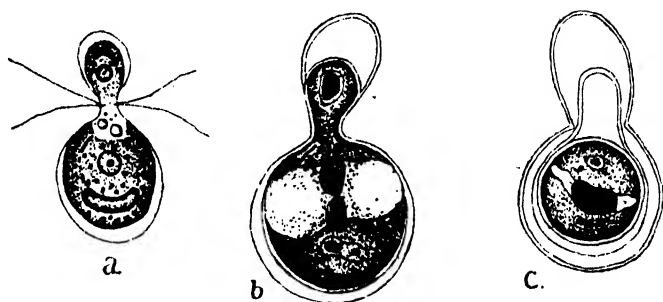


FIG. 45.—Conjugation of *Chlamydomonas braunii*. *a*, small male and larger female gametes beginning to fuse; *b*, fusion begun but nuclei (equal in size) and chloroplasts still separate, the gametes are forming new walls within the old; *c*, nuclei fused but separate chloroplasts still visible at top and bottom. The zygote wall is beginning to form. After Goroschankin.

**Sex Differentiation.** When the gametes are all of equal size, as they are in many species of *Chlamydomonas*, they are called *iso-gametes*. In some species the gametes are of varying sizes owing to the differing numbers of divisions which formed them. Conjugation may then occur irrespective of size; but in some species *anisogamy*<sup>2</sup> occurs, i.e. only gametes of different sizes fuse together. *Chlamydomonas braunii* Gorosch. performs relatively few divisions in gamete formation. It produces four *macrogametes*<sup>3</sup> from a single mother cell or eight *microgametes*.<sup>4</sup> The macrogametes have the same structure as a normal cell but the microgametes are about half the size and relatively long and narrow. The macrogametes come to rest without losing their flagella while the microgametes continue to move about actively. When two gametes of unequal size come into

<sup>1</sup> Greek ἴσος (isos), equal.

<sup>3</sup> Greek μακρός (makros), large.

<sup>2</sup> Greek prefix α- ἀν- (a-, an-), not.

<sup>4</sup> Greek μικρός (mikros), small.

contact at their anterior ends, the cell walls become fused together. The protoplasm of the smaller gamete separates from its wall and passes over into the larger, sometimes secreting a new wall round its hinder end (Fig. 45). The flagella disappear while fusion is going on, and the zygote is formed within the cell cavity of the larger gamete.

Here we have two leading characters of the sexual differentiation of gametes appearing—a difference in *size* and a difference in *activity*. Though both gametes begin life as free-swimming cells of identical structure, one is more active than the other in the act of conjugation. The difference of activity seems to be here a mere mechanical result of the difference in size. If we suppose the protoplasm of each gamete to be attracted equally strongly towards the other, the body of the small one would be the more easily drawn through the narrow canal connecting them. A third difference, that of *structure*, is hardly shown by *Chlamydomonas* gametes but is shown in other algæ such as *Volvox* and *Fucus* (p. 130).

In the following organisms the cells do not live singly, like *Chlamydomonas*, but remain together surrounded by a common mucilaginous envelope. Each cell has the same essential structure as a *Chlamydomonas* cell, and the flagella protrude outwards through the mucilage. Such a colony, consisting of a fixed number of cells arranged in a specific manner and forming a definite integrated whole, is called a cœnobium.<sup>1</sup> It behaves like a single organism, moving through the water by the co-ordinated beating of the flagella of all the cells.

#### PANDORINA

*Pandorina* is a more or less spherical cœnobium, usually containing sixteen cells which are pressed closely together so that each cell is somewhat wedge-shaped. The cœnobium has a fixed polarity, one pole always being directed forward (Fig. 46). The chloroplast is cup-shaped and has a pyrenoid. Each cell has two equal flagella, two contractile vacuoles and an eye-spot at the broad outer end.

#### Reproduction

*Asexual.* Just before reproduction begins the cœnobium becomes immobile and the envelope absorbs water and swells. All the cells divide simultaneously to sixteen daughter cells, each group constituting a new cœnobium (Fig. 46 B). The sixteen young cœnobia swim out of the watery mother envelope and grow to full size.

<sup>1</sup> Greek κοινός (koinos), common and βίος (bios), life.

*Sexual.* The formation of gametes takes place by similar divisions; but they proceed to various extents so that anisogametes of differing sizes are formed. They leave the mother colony in cœnobium-like masses which shortly after break up and release gametes having no cell wall (Fig. 46 C). Conjugation occurs between free-

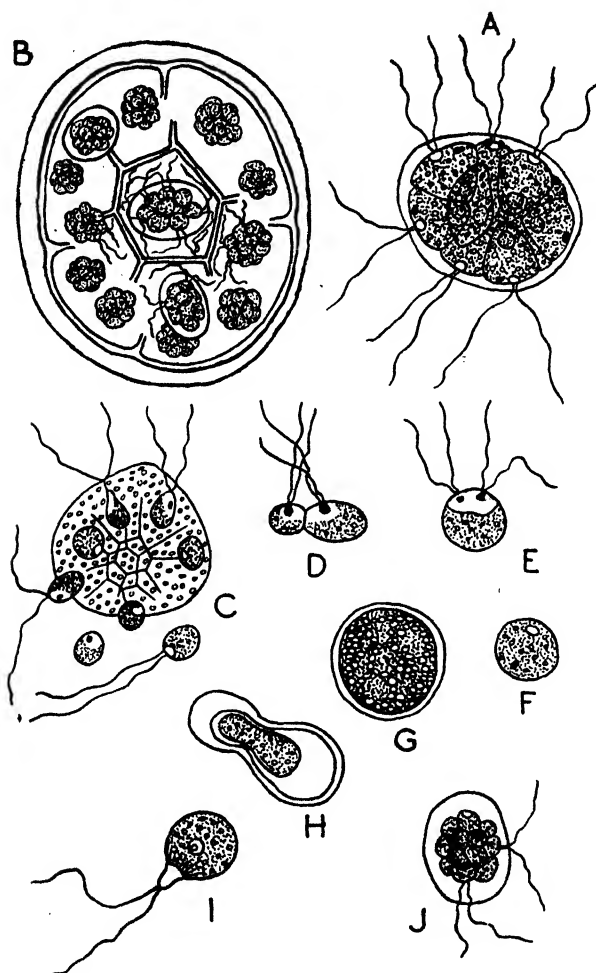


FIG. 46.—*Pandorina*. A, cœnobium of 16 cells with anterior end to the left. B, asexual formation of 16 daughter cœnobia inside the parent envelope. C, gametes escaping from mucilage. D and E, fusion of unequal gametes. F and G, zygote formation. H, zygote protoplast breaking out of the thick wall to form I, biflagellate zoospore. J, daughter cœnobium formed by divisions of the zoospore. After Pringsheim.

swimming gametes of the same or different sizes. The larger, female gametes may be more sluggish than the smaller male ones and may even remain within the mucilaginous envelope. Fusion may occur end to end or side to side. The zygote continues to swim for a short time with its four flagella, then settles down, loses its flagella and develops a wall and red coloration (Fig. 46 G). On germination, the protoplast escapes from the thick wall (Fig. 46 H) as a single bi-flagellate zoospore. After swimming freely for some time it retracts its flagella, secretes a gelatinous envelope and divides to form a complete colony (Fig. 46 J).

## EUDORINA

The cœnobia of *Eudorina* are spherical or ellipsoidal. They are larger than *Pandorina* and have thirty-two or sixty-four cells according to species. The cells are always arranged in a single layer on the

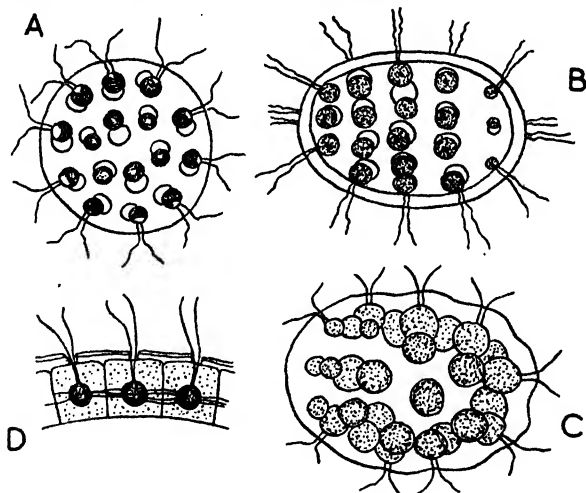


FIG. 47.—A, *Eudorina elegans*, cœnobium of 32 cells. After West. B, *Eudorina illinoiensis*, anterior end to right. After Kofoid. C, *Eudorina indica*, anterior end to left. After Iyengar. D, optical section of surface of *E. elegans* showing protoplasmic fibrils connecting the cells, and blocks of mucilage secreted from each. After Schewiakoff.

surface of the hollow cœnobium and frequently lie in regular rows across the short axis of the ellipsoid (Fig. 47 A). The individual cells have the *Chlamydomonas* type of structure; but are spherical and the flagella are relatively long, two to four times the length of the cell. They project through the mucilage of the envelope and move the cœnobium, which has definite orientation as in *Pandorina*, by their

106 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA co-ordinated movements. All the cells have eye-spots which in some species of *Eudorina* become progressively smaller from the front to the rear end of the colony. The cells are connected to one another by

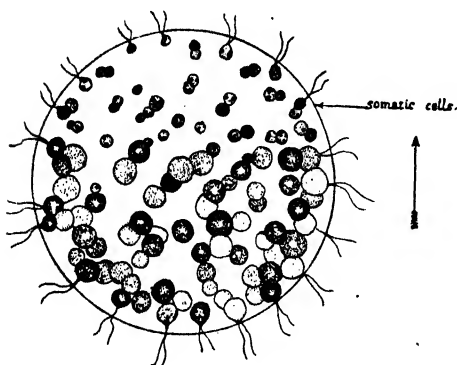


FIG. 48.—*Pleodorina californica*. Cœnobium showing numerous somatic cells at the anterior end.

very fine fibrils of cytoplasm passing through the mucilage. These appear to be withdrawn as the organism matures.

### Reproduction

*Asexual.* Individual cells of the cœnobium divide to form daughter cœnobia, as in *Pandorina*. One of the most interesting things about the reproduction of *Eudorina* is a progressive specialisation

among the cells of the colony shown by different species. In the simplest, *Eudorina elegans*, all cells are capable of division; though four, at the anterior end, are frequently more sluggish about it than the remainder. In *Eudorina illinoiensis* (Fig. 47 B) these four cells remain permanently smaller than their fellows and frequently do not divide at all. In *Eudorina indica* (Fig. 47 C) the front two tiers of

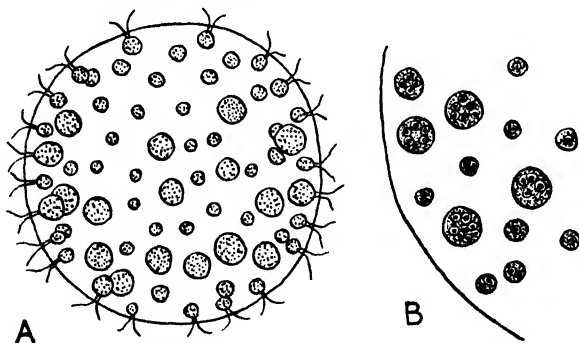


FIG. 49.—*Pleodorina sphaerica*. A, cœnobium showing somatic cells scattered about. B, part of cœnobium further enlarged.  $\times 660$ . After Iyengar.

cells remain permanently small. This process goes even further in the allied genus *Pleodorina* which is like a larger *Eudorina* with more numerous cells in the colony. In *Pleodorina californica* (Fig. 48) about half its cells, all situated at the front, remain purely vegetative;

and in *Pleodorina sphaerica* many of the cells in the rear half of the cœnobium are vegetative also.

*Sexual.* The same series of reduction of dividing cells is shown as in asexual reproduction. There is also a well-marked distinction between male and female gametes. In some species male gametes are produced by division of the small anterior cells, the large posterior cells forming eggs without division. The male gametes are formed by repeated divisions to give sixty-four spindle-shaped *sperms*,<sup>1</sup> each

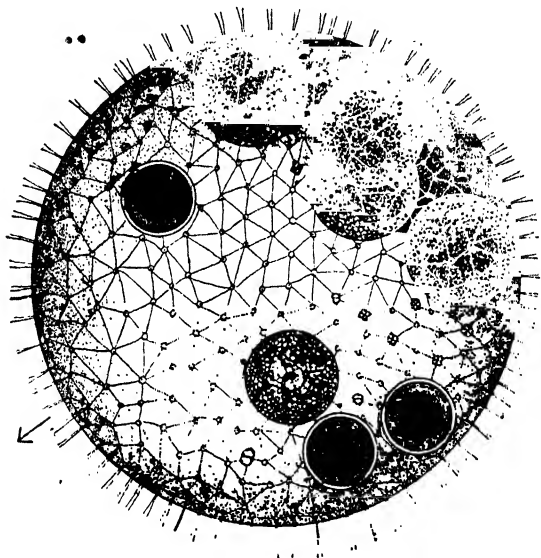


FIG. 50.—*Volvox aureus*. A cœnobium showing fertilised eggs with walls, groups of small cells dividing to form sperms, and large spheres which are young cœnobia produced asexually. The front quadrant, indicated by the arrow, has no reproductive cells.  $\times 180$ . After Klein.

with two flagella and a yellow coloration at the hinder end as a vestige of the chloroplast. In other species of *Eudorina* the sperms and eggs are produced in different cœnobia, and pockets of sperms escape from the remains of the male cœnobium, swimming as a unit until they reach a female colony. Here they break up into single male gametes, and swim into its swollen mucilaginous envelope. Apart from the swelling of the envelope there is not much change in the female colony, its cells behaving as female gametes without division,

<sup>1</sup> Greek σπέρμα (sperma), seed. This is a useful term applied to the male gametes both in animals and plants. The male fertilising element has often been called the "seed" in common language.

108 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA though they lose their flagella and may become a little larger. The mature zygote has a thick wall and is coloured red. When germinating it puts out a thin-walled sac on one side from which a zoospore escapes. After swimming for a time the zoospore divides repeatedly to form a new colony.

#### VOLVOX

*Volvox* is the largest and in many respects the most highly differentiated of this series of organisms. It may attain about half a millimetre in diameter and appear to the naked eye as a grey speck against a dark background (cf. Table on p. 35). It may have as many as 20,000 cells in a single cœnobium, all arranged upon the surface of

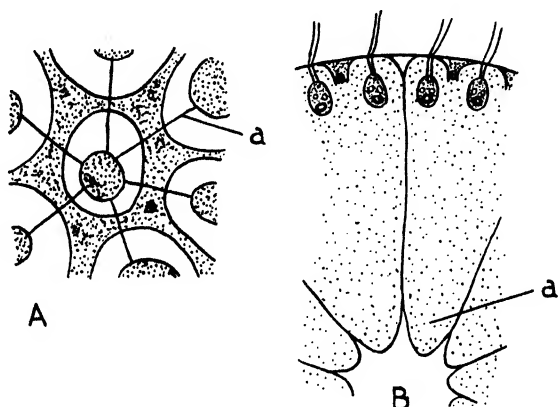


FIG. 51.—*Volvox aureus*. A, part of surface showing protoplasmic fibrils, *a*, connecting cells through the mucilage. B, sectional view showing *a*, wedges of mucilage with cells embedded near their surface. After Meyer.

the hollow mucilaginous sphere (Fig. 50). The individual cells of *Volvox aureus* (Fig. 51) are of chlamydomonadine structure, with two flagella, a cup-shaped chloroplast and a pyrenoid. The nucleus is placed at the centre of the cell. Each cell has a single eye-spot (Fig. 43 B) placed at the outer surface and cells at the anterior end of the colony usually have larger eye-spots than those towards the rear. Instead of the usual two contractile vacuoles near the insertion of the flagella, the cells have five or more distributed throughout the cytoplasm. There are fine cytoplasmic fibrils connecting the cells (Fig. 51 A) through the mucilage, which extends in wedge-shaped masses towards the interior (Fig. 51 B). These details are different in other species.

*Reproduction*

**Asexual.** The great majority of the cells of *Volvox* are vegetative only and incapable of reproduction. Some 5–20 cells capable of asexual reproduction are situated in the rear half of the cœnobium. These swell to ten or more times the size of the vegetative cells and then divide repeatedly in the longitudinal planes until a hollow sphere is formed (Fig. 52 a–f). When cell division stops, the anterior ends of all the cells (which will bear the flagella) are directed in-

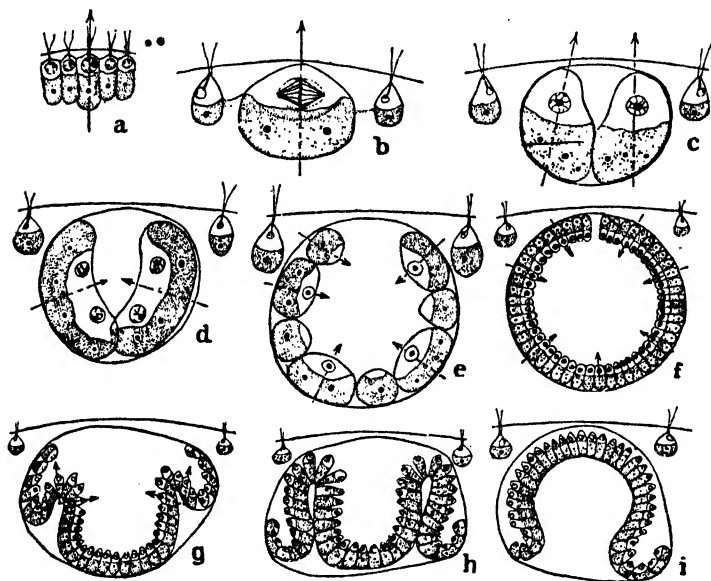


FIG. 52.—*Volvox aureus*. Stages in the asexual formation of a daughter colony. *a* and *b*, the enlarging and dividing spore, shown by the arrow; *c*, first division complete; *d–f*, further divisions forming a complete new sphere except for a small pore towards the surface of the colony. The anterior ends of the cell are all pointing in towards the centre of the new colony; *g–i*, stages showing the new colony turning completely inside out, thus bringing its flagella to the outside. After Klein.

wards, and the young colony proceeds to turn itself inside out (Fig. 52 *g–i*), taking three to five hours to do so. The pore does not close up but remains open at the anterior end. Flagella then develop and the young colony rotates within the much-stretched wall of the parent cell. It escapes into the interior of the mother colony, where it usually remains for some time and may even produce a third generation while still enclosed. The final liberation usually involves the irregular tearing open of the parent which then dies.



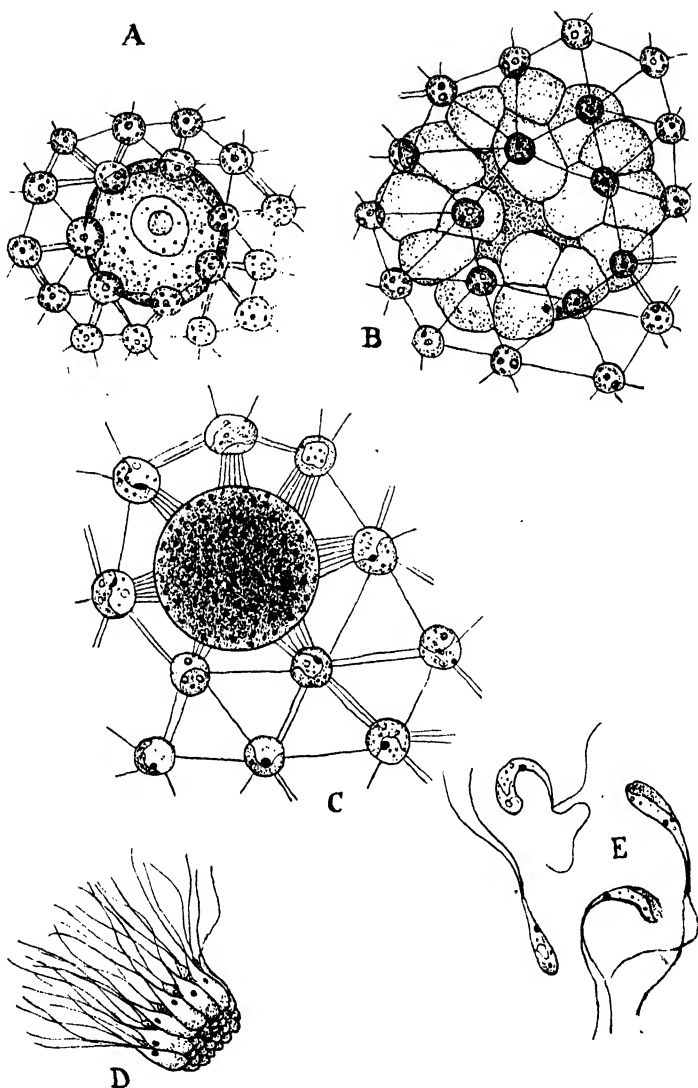


FIG. 53.—*Volvox aureus*. A, part of the surface of a cœnobium showing vegetative cells joined by fibrils, and a spore.  $\times 550$ . B, partly grown daughter cœnobium formed by divisions of the spore.  $\times 550$ . C, egg with protoplasmic fibrils to neighbouring vegetative cells.  $\times$  about 700. D, isolated plate of sperms.  $\times 700$ . E, individual sperms showing chloroplast, eye-spot and flagella.  $\times 825$ .

*Sexual.* Differences of structure, activity and size between the male and female gametes of *Volvox* are very considerable. The male gametes are formed by cells called *antheridia*.<sup>1</sup> Each of these divides repeatedly to give a flat plate of small long-conical sperms (Fig. 53 D and Fig. 54 A), very similar in appearance to the sperms of *Eudorina*. The female, or egg, cells are dotted about the hinder end of the cœnobium, projecting inwards on account of their large size (Fig. 53 C and Fig. 54 B). There are no cell divisions in their formation and each corresponds with a single germ cell. They have no flagella, but are copiously stored with reserve substances and remain in protoplasmic connection with the surrounding somatic cells, from

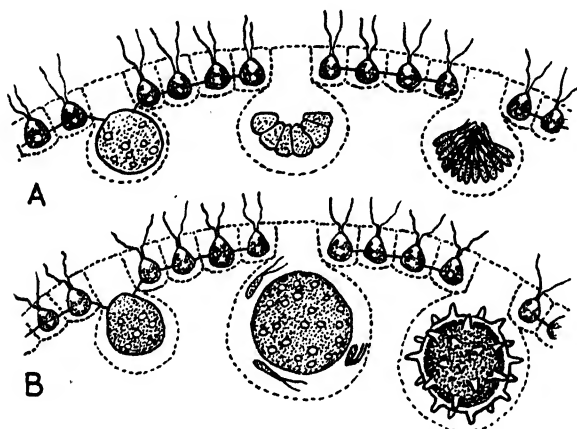


FIG. 54.—*Volvox* sp. A, divisions of an antheridium forming sperms. B, egg, fertilisation and zygote. After Smith.

which they may be able to derive still further supplies (Fig. 54 B, left-hand side). These passive egg cells remain attached to the cœnobium and may be fertilised by sperms from the same cœnobium or another. The entire mass of 64–128 sperms from an antheridium usually swims as a colonial unit until it approaches an egg (cf. *Eudorina*, p. 107). Individual sperms enter the wall of the egg (Fig. 54 B, centre) and bring about fertilisation. After the fusion the egg forms a zygote (Fig. 54 B, right-hand side) with a thick wall and a dark red coloration. The zygote is only liberated by the break-up of the parent cœnobium. Germination may be delayed for several months or even years and is preceded by a reduction division (p. 148)

<sup>1</sup> Greek ἀνθήρα (anthēra), flowering. The name antheridium is applied to organs producing sperms in all classes of plants.

112 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA of the zygote nucleus. After the zygote of *Volvox aureus* escapes from the thick wall its protoplast develops directly into a new colony by repeated divisions. In other species a biflagellate zoospore is formed which only forms a new colony after a period of free-swimming (cf. *Eudorina*, p. 108).

### *The "Soma" in Plants and Animals*

The evolution of a soma or mortal body is beautifully illustrated in the *Pandorina-Eudorina-Pleodorina-Volvox* series. This evolution consists essentially in the separation of the vegetative and reproductive functions. In the lower forms of the series all the cells of the body discharge both functions; but in the higher members some cells discharge the vegetative, others the reproductive function. Directly we have any cells limited to the vegetative functions, we have a soma or mortal body by the very fact that these cells can no longer reproduce the species.

It must be noted, however, that this particular series of organisms is not in the direct line of evolution of any of the higher organisms. *Volvox* is the culmination of its own line of descent. It is probable that no further increase in size or complication is possible to the motile cœnobiate form of organism. The soma has been evolved on many other lines of descent from unicellular organisms. This particular line is chosen for illustration because of the existence of several forms which make up a closely connected series; and midway in this series *Pleodorina* shows the actual first appearance of the soma, *P. illinoiensis* being a very slight modification of the *Eudorina* type.

All the multicellular animals have a well-marked soma, i.e. a body consisting of tissues whose cells are not germ cells and which do not reproduce the species by spore or gamete formation. In many of the lower invertebrates new individuals are produced by budding of those somatic tissues which are not too highly specialised for the performance of a vegetative function. In the higher animals budding falls into abeyance, and the life of the somatic tissues is strictly limited to the service of the individual of which they are a part, and comes to an end with its life.

In plants, however, the power of reproducing the species is much more often retained by the cells of the vegetative body. In filamentous green algæ, like *Spirogyra* (p. 117), all, or nearly all, the cells of the multicellular thread of which the body is composed retain the power of forming zoospores or gametes and thus may be

"germ cells." In the bulky algæ (seaweeds) as well as in all the higher plants, this power is lost by the general mass of body cells. The plant may, nevertheless, be reproduced vegetatively by processes analogous to the budding of the lower animals, quite independently of the germ cells proper. This power of "vegetative reproduction" is retained by some at least of the body cells of practically all plants, even the highest and most complicated forms, as we shall see in later chapters.

Taken together these facts show us that the distinction between somatic and germ cells is not an absolute one. Though the germ cells (spores and gametes) are the specialised reproductive cells whose *sole* function is to reproduce the species, this power may be retained by

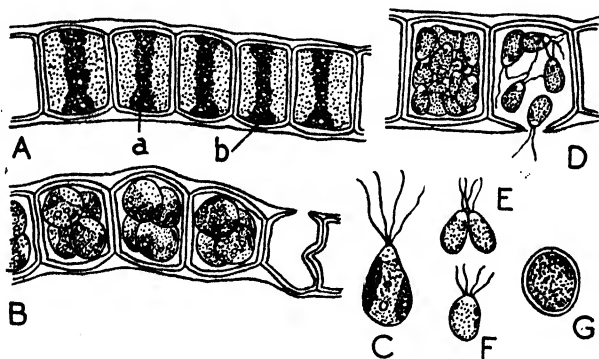


FIG. 55.—*Ulothrix zonata*. A, part of filament; *a* and *b*, chloroplasts. The minute white dots in the chloroplasts are pyrenoids. B, cells forming groups of 4 zoospores. C, a zoospore with 4 flagella. D, the cell on the left has produced numerous small spores, on the right biflagellate spores are escaping. E and F, gametes fusing. G, zygote. After Smith.

the body cells to a varying extent in different organisms. The body cells of plants retain it far more generally than those of animals, and this is undoubtedly connected with the fact that plant cells are, in general, far less highly modified for the performance of special functions than the cells of the higher animals.

#### THE FILAMENTOUS ALGÆ—ULOTHRIX

*Ulothrix zonata*<sup>1</sup> is a characteristic alga of flowing fresh water and forms bright green masses attached to stones. It is particularly abundant in the cool waters of spring and autumn. The cells of the filament, which is unbranched, are shorter than they are broad and

<sup>1</sup> From Greek ζώνη (zōnē), girdle; referring to the chloroplast.

114. THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
the chloroplast forms a simple girdle round the cell (Fig. 55 A). It contains several pyrenoids and there is a single central nucleus. All the cells are of this simple pattern except the basal one which forms a holdfast. Multiplication may take place by the breaking up of the filament.

### Reproduction

*Asexual.* All cells, except the holdfast, are capable of reproduction which usually sets in towards the apex of the filament. The

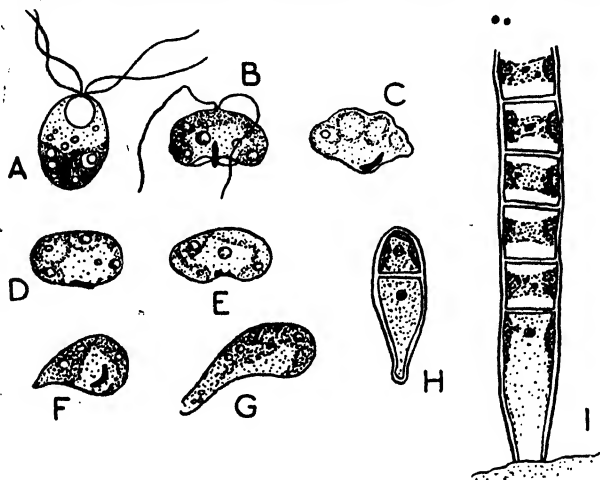


FIG. 56.—A-E, large zoospore settling down. F and G, germination. After Goss. H, first division by a cross wall to form a filament and a holdfast cell. I, young filament after further divisions of the upper cell.

protoplast contracts slightly and becomes filled with food materials. The nucleus divides and the cytoplasm after it to form eight or more zoospores. The interesting thing is that these have a structure strongly reminiscent of the *Chlamydomonas* type (Fig. 55 B and C), though without walls (resembling *Chlamydomonas* gametes) and often with four flagella.<sup>1</sup> These zoospores escape from the mother cell in which they were formed through a pore in the side wall (Fig. 55 D). They swim about for a time and then settle down on some solid object, lose their flagella and germinate by secreting a cell wall. They broaden out (Fig. 56 D and E) to form an attachment at the posterior end and divide (Fig. 56 H) to form a filament at the

<sup>1</sup> *Carteria* is a free-swimming quadriflagellate otherwise identical with *Chlamydomonas*.

anterior end. The zoospores of *Ulothrix zonata* are of two sizes. The larger ones always have four flagella and move about for a shorter period than the others, usually less than twenty-four hours, before settling down. We may consider that in its reproduction, *Ulothrix* reverts to the condition of a *Chlamydomonas*-like ancestor; or to put it the other way round, that a *Chlamydomonas*-like ancestor settled down and divided repeatedly without separation of the daughters. By this means a thread of cells, all of which still retained the capacity to produce a brood of chlamydomonadine cells in reproduction, was perhaps started.

*Sexual.* The gametes of *Ulothrix* are similar to the zoospores but smaller. They are biflagellate and fuse in pairs (Fig. 55 E and F). There is no differentiation of size, shape or activity, but gametes of one filament only fuse with those from another. The zygote (Fig. 55 G) remains motile for a short time, settles down, secretes a thick wall and enters a resting phase. Its first division is a reduction division, and further segmentation then leads on to the formation of zoospores which, like zoospores asexually produced, give rise to new filaments. This procedure is similar to the behaviour of the zygotes of the colonial types (p. 112).

#### SPIROGYRA

*Spirogyra* is an alga that floats freely without attachment of any sort on the surface of freshwater pools. It is easily distinguished from other filamentous algæ in the same situation by its clear, deep green colour and its silky feeling, due to the coating of mucilage that is continuous over its surface. The body of the plant consists of an unbranched thread composed of cylindrical cells, usually longer than they are broad, joined end to end. All the cells are alike and there is not even a specialised attachment cell, as in *Ulothrix*. Each cell has a large central vacuole, resembling in this the great majority of plant cells, but differing from *Protococcus* and the *Chlamydomonas* type of cell, which is entirely filled by protoplasm with its nucleus at the centre. The nucleus of a *Spirogyra* cell is also situated at its centre, but is suspended in the vacuole by protoplasmic bridles (Fig. 57 B). Embedded in the thin layer of cytoplasm lining the wall is the large spiral chloroplast or chloroplasts from which the genus takes its name. In cells having more than one chloroplast the spirals run in parallel. The crossing lattice-structure, seen when the cell is looked through from above, is due to the fact that the parts of the chloroplasts which run round the farther, lower side of the cell are seen at

116 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
 the same time as the parts on the upper side towards the observer.  
 By careful focusing upon the upper and lower sides of the cell in  
 turn, this can be made clear. The chloroplasts have wavy edges and

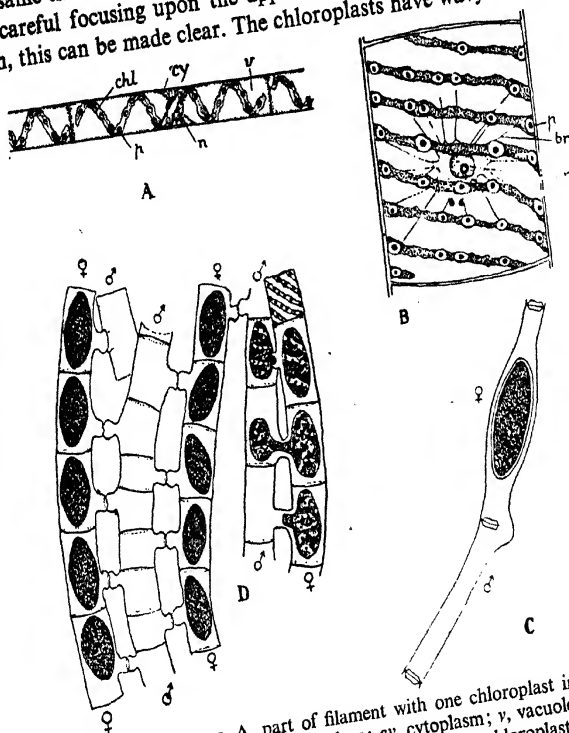


FIG. 57.—*Spirogyra*. A, part of filament with one chloroplast in each cell; chl, chloroplast; p, pyrenoid; n, nucleus; cy, cytoplasm; v, vacuole. B, surface view of a cell of a larger species with more than one chloroplast in the cell; chl, chloroplast; p, pyrenoid.  $\times$  about 550. C, zygote formed by conjugation of gametes from adjacent cells of the same filament; the male gamete moves from the empty cell marked ♂ into the female cell ♀. D, five filaments that have taken part in conjugation. Stages of the movement of the male gamete are shown on the right and newly formed zygotes on the left. Filaments behaving as males are marked ♂ and females ♀. After West, modified.

numerous pyrenoids scattered along their length (Fig. 57 A and B), which are frequently linked by protoplasmic bridges direct to the nucleus. This suggests a function for the nucleus in controlling the cells' syntheses, since it is round the pyrenoids that starch is laid down (cf. also p. 49).

#### Cell Division

The nuclei of *Spirogyra* cells divide mitotically (p. 51), and cell division follows immediately. Any cell may divide, its position in the

filament making no difference. As soon as the formation of the daughter nuclei is complete, the spindle, instead of disappearing, begins to spread out towards the side walls of the cell. At the same time a thickened ring of cytoplasm forms inside the wall and the two growths finally coalesce (Fig. 29, p. 57). Within this special protoplasmic formation a thin septum is rather suddenly produced. It starts forming at the walls and closes in like an iris diaphragm. The chloroplasts are cut in two by its progress and cellulose thickenings are afterwards deposited on each side.

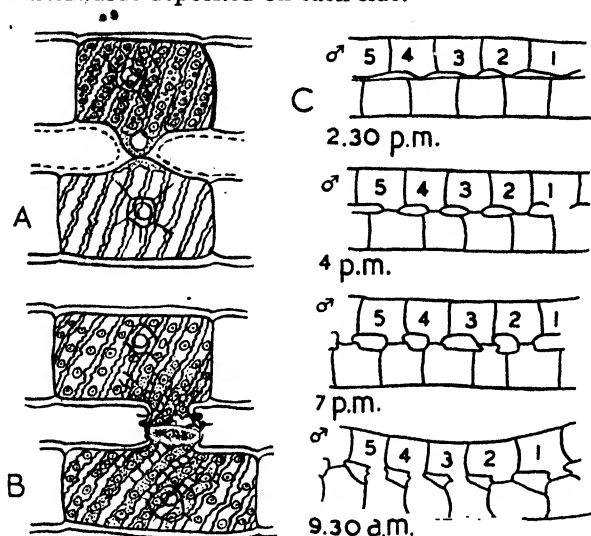


FIG. 58.—A and B, *Spirogyra setiformis*, formation of the conjugation canal. After Czurda. C, time sequence of canal formation. After Saunders.

**Fragmentation of the Threads.** The middle lamella joining *Spirogyra* cells frequently breaks down, with the result that the filament is divided up into several shorter ones which then go on growing by further cell divisions. It is of little moment to the cell whether it is joined in a long or short filament, and *Spirogyra* is sometimes described as “physiologically unicellular” because each cell functions as a self-contained unit.

### Reproduction

The reproduction of *Spirogyra* is by means of gametes and occurs between two or more filaments lying side by side and becoming glued together by mucilage. Conjugation is carried out only by cells that have recently divided. One cell of each opposite pair puts out a



118 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
 papilla and usually the papillæ all appear on one filament (Fig. 58  
 A and C). A little later corresponding papillæ arise on the opposite  
 filament and as they all enlarge the conjugation canal is formed,  
 pushing the two threads a little apart. When this is complete, the two  
 cross walls are dissolved and the conjugation canal is open. The arms  
 of the two protoplasts that have extended into the canal are thus

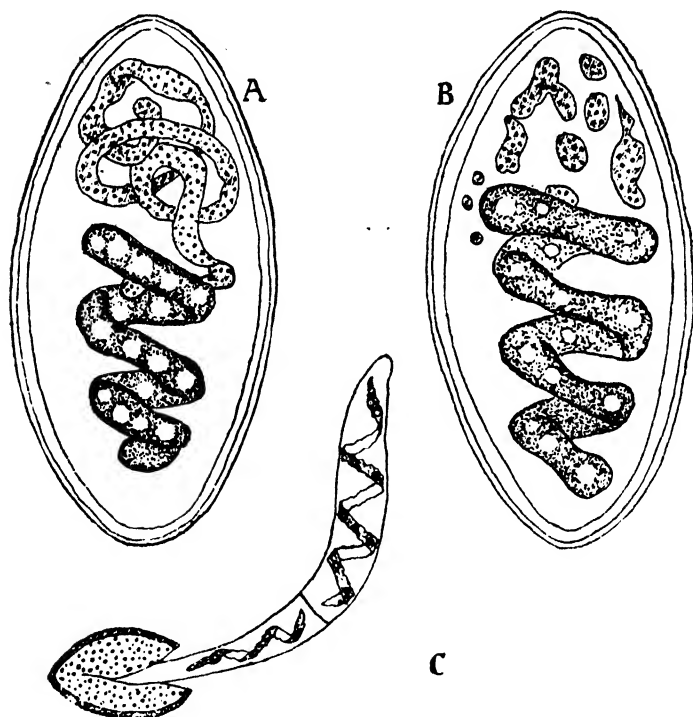


FIG. 59.—*Spirogyra*. A and B, development of the zygote; the male chloroplast (above) is shown degenerating and breaking up. The chloroplast of the female gamete persists and produces the chloroplasts of the new individuals.  $\times 800$ . After Chmielevsky. C, germination of the zygote; two cells of the new filament emerging from the split wall of the zygote.  $\times 400$ .

brought into direct contact (Fig. 58 B). The two protoplasts remain continually in contact from this moment and one of them, the male, begins to shrink away from the wall of its own cell and gradually to pass through the conjugation canal, fusing with the contents of the other, female, cell. When fusion is complete the united protoplast begins to shrink away from the cell wall (Fig. 57 D), liquid probably being secreted by means of contractile vacuoles. The struc-

ture of the individual chloroplasts disappears, the male usually being lost first, and a new cell wall is formed in three layers (Fig. 59 A and B). The zygote thus produced contains much fat and is often coloured red. In this scalariform<sup>1</sup> method of conjugation one filament may be distinguished as the male, since its gametes move towards the still, or female, gametes. Sometimes when three or more filaments are lying alongside one another the middle filament may act as male towards one partner and female towards the other, and the idea of relative sexuality arises (cf. p. 121). Occasionally lateral conjugation takes place between cells adjoining one another

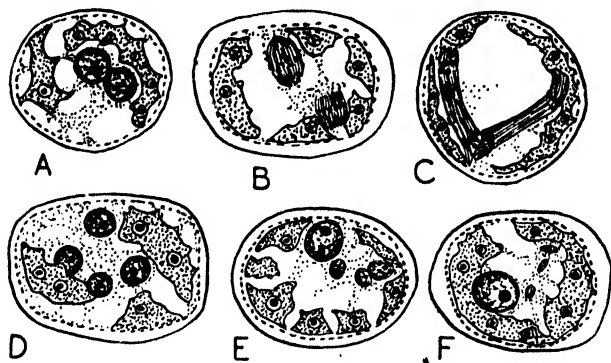


FIG. 60.—*Spirogyra longata*. Maturation of the zygote. A, two daughter nuclei of the first (reduction) division. B and C, second nuclear division. D, four daughter nuclei. E, degeneration of 3 nuclei. F, single nucleus surviving. After Tröndle.

in the same filament and there is no sexual differentiation between filaments at all (Fig. 57 C). Some cells are more female than their neighbours which are relatively male. A protrusion of the side walls develops in continuous contact on both sides of the dividing septum and the male protoplast passes, or is drawn, through to the female just as in scalariform conjugation.

The gametes of *Spirogyra* and its allies have no flagella and the movement of the males may be labelled amœboid, but its mechanism is obscure. It is possible that once the two protoplasts have established contact by the solution of the dividing wall, their fusion and rounding off is largely due to surface tension.

The zygote is a dormant stage, as in other species, and the fusion of the gamete nuclei may not take place immediately. Before actual germination, the fusion nucleus divides twice, the first being a

<sup>1</sup> Latin, *scalae*, ladder.

120 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA reduction division (p. 148). Only one of the four daughter nuclei survives (Fig. 60). The fat stored in the zygote changes to starch (as during the germination of fatty seeds). The chloroplast becomes distinct and the two outer coats of the zygote are ruptured. The contents grow out surrounded by their inner coat and divide into two cells (Fig. 59 C). Subsequent growth of the filament results from further divisions of the upper cell.

*Parthenospores.* Sometimes the conjugation process appears to be interrupted or to fail at some intermediate stage. In *Spirogyra grænlandica*, after the conjugation papillæ have joined up, but before their end walls have been dissolved, the protoplasts round off and secrete new membranes. In *Spirogyra mirabilis*, similar spores are formed without any preliminaries of conjugation. They are able to germinate like zygotes and are called parthenospores<sup>1</sup> to indicate that no sexual act has occurred in their production.

#### *Nature and Significance of Sexual Differentiation*

The wide difference in structure and function between the male and female gametes of *Volvox aureus* is repeated in the sexual reproduction of the vast majority of plants and animals. The sperm is exceedingly sensitive, at least in many species, to chemical substances diffusing out of the female gamete. Sperms are produced in immense numbers and only a minute proportion succeed in conjugating with the eggs. The body of the sperm is reduced to the smallest size compatible with its function, which is to carry the paternal nucleus to the egg. Its chromosome contribution to the zygote nucleus—and hence its effect upon the character of the offspring—is equal to that of the egg nucleus. The egg, on its side, supplies the immediate provision of organic food with which the new individual starts its life, and the relatively large size and the passivity of the female gamete are correlated with this function. Owing to the fewer cell divisions during their formation, and the larger quantities of material consumed in their formation, far fewer eggs are produced than sperms. Reduction of the sperms is carried even further in the higher plants, where they no longer depend upon their own flagella to convey them to the eggs (p. 303), and the eggs provide nourishment more efficiently by remaining within the parent body instead of accumulating it in their own cytoplasm.

If we were to confine our studies to such sexually perfected types, we should naturally regard sexual differentiations as something hard

<sup>1</sup> Greek παρθένος (parthenos), virgin.

and fast, and maleness and femaleness as absolute characters. Widening our knowledge soon dissipates this simple outlook. The sex of *Spirogyra* filaments is relative rather than definitive (p. 118). The comparatively slight differences between the gametes in *Chlamydomonas* and *Pandorina* appear as a result of merely accidental differences in the rapidity and duration of the divisions of a mother cell. When the divisions are rapid and numerous small (male) gametes are produced; fewer divisions give female gametes which are larger but still of identical structure. The sluggishness of the larger gametes, especially of *Pandorina*, is probably merely a result of their larger size; but they obviously contain the first elements of femaleness as it exists in the higher forms. This "casual" origin of sex is an excellent example of the beginning of a differentiation which is accidental, as it were, i.e. without reference to its ultimate use; but which later becomes fixed by selection and adaptation and eventually develops into a more or less efficient working mechanism. The more we learn of the evolution of structure and function in organisms the more we find that something like this is the history of the evolution of new characters.

In passing from the casualness of the most primitive forms to the sharp distinctions of the more advanced, several conditions, convenient for purposes of arrangement, may be recognised.

*Isogamy.* The conjugation of gametes of equal size and similar structure is named isogamy. It is common in *Chlamydomonas* and typical of *Spirogyra*. Isogametes are usually naked protoplasts without walls (see pp. 114 and 118). Although the isogametes of a particular species are all alike in appearance, they may have different properties. In the genus *Zygnema*, closely allied to *Spirogyra*, conjugation of equal gametes takes place in the conjugation-tube; the gametes behave as well as look alike. The isogametes of *Spirogyra* itself are divided by their degree of motility into male and female and may show other minor signs of differing sexuality such as the earlier degeneration of the chloroplasts in the males. Even where such distinctions as this fail, there may yet be functional differences among isogametes, because those produced by a single parent cell are rarely able to conjugate among themselves. Such organisms in which conjugation only occurs between the gametes of different parents are termed *diæcious*.<sup>1</sup> They are not said to possess male and female sexes, but positive and negative strains.<sup>2</sup> In primi-

<sup>1</sup> Greek δι- (di-) twice; οἶκος (oikos) housed; cf. such flowering plants as holly.

<sup>2</sup> See page 365 for an example among the Fungi.

122 THE GREEN ALGÆ: ORIGIN OF SEX AND OF THE SOMA  
tive plants the opposite strains may be produced in equal numbers at the time of the reduction division; that is to say their production is *genotypic*, or determined by the hereditary material of the cell. Sometimes fragments of *Spirogyra* filaments may give rise to plants of either sex which must, therefore, be determined *phenotypically*, i.e. by the circumstances of their environment.

*Anisogamy*.<sup>1</sup> Among the free-swimming gametes of *Pandorina*, conjugation often occurs between partners of somewhat unequal size, though otherwise identical appearance. This is termed anisogamy. It appears to be a matter of chance whether the partners are equal or not. Many *Chlamydomonas* species behave in the same way; but in *Chlamydomonas braunii* (p. 102), conjugation only occurs between smaller (male) gametes and larger (female) ones. The latter are sluggish, tending to settle down at an early stage, and in this species anisogamy has become fixed.

*Oogamy*.<sup>2</sup> Oogamy involves the complete differentiation of gametes into large immobile eggs and small active sperms. It occurs in *Chlamydomonas coccifera*, so that the whole range of gametic specialisation is represented within the confines of a single large genus. Oogamy is, however, much commoner in the multicellular cœnobiote and thalloid (see *Fucus*, p. 130) algæ; and indeed among the higher plants generally. There is no sharp division between isogamy, anisogamy and oogamy, but an infinite series of graded forms and relative sizes.

### Practical Work

The material for this practical work may have to be varied according to what can be obtained. *Chlamydomonas* is generally available during the warmer months, appearing in rain-water butts, bird-baths and other standing receptacles. It is easily concentrated by gentle centrifuging or filtration and a hunt through such a concentrate will usually reveal a proportion of the simpler cœnobiote forms. *Spirogyra* must be sought on quiet ponds and *Ulothrix zonata* on stones in flowing waters. It is oftenest found in spring and autumn.

*Chlamydomonas* can be maintained in open tubs containing tap water enriched with a few grams of sodium phosphate, potassium sulphate and ammonium nitrate per gallon. An inoculum of pond mud may help and contamination by occasional falling leaves and small insects does no harm. When a good green colour (*Chlamydomonas*) has developed, it helps to add a lump or two of sugar. The culture can be maintained so long as sugar and ammonium nitrate are occasionally added. *Pandorina* is encouraged by the addition of protein as lumps of dried egg albumin. *Eudorina* may also appear, but is sporadic. Failing all else, material may be obtained from the botanical supply agencies. The formation of a small collection of permanent slides showing different stages of the life cycle is desirable.

<sup>1</sup> Greek, αν (an-), not; ισος (isos), equal.

<sup>2</sup> Greek ωον (ōon), egg.

## A. CHLAMYDOMONAS—VOLVOX

(1) Observe a drop of concentrated *Chlamydomonas* suspension under the low power. Turn to the high power and examine a specimen at rest. The flagella often get stuck to the slide or coverslip and the cell thus anchored oscillates to and fro. Note the *cell wall*; the basin-shaped *chloroplast* and its *pyrenoid*; the clear front end with the attachment of the *flagella*; and the red *eye-spot*. This may appear to "come and go." Hunt for stages of division. Run a drop of dilute iodine under the coverslip and examine again. The cells, being killed, will remain still and some details of their structure become easier to observe.

(2) Examine a demonstration specimen set up under an oil-immersion lens for other organelles such as the *nucleus*.

(3) Examine specimens of *Pandorina* and *Eudorina* (preserved material if fresh cannot be obtained), noting the construction of the cœnobium and the fact that the structure of each cell is of the *Chlamydomonas* type. Examine also stages of division to form daughter cœnobia, if these are available.

(4) Observe with the naked eye the large spherical cœnobia of *Volvox aureus* (on the whole the commonest species) in a drop of water on a slide placed on a piece of black paper. Examine under the low power without a coverslip. Note the large reproductive cells or daughter cœnobia. Put a coverslip very gently over the preparation and examine under the high power. If sexual colonies are present, note developmental stages of sperms and eggs.

(5) Examine a single vegetative cell under the high power and note that it is of *Chlamydomonas* type. Run in a drop of iodine and look for the *flagella* and threads of *cytoplasm* connecting the cells.

## B. ULOTHRIX

(6) Examine a filament of *Ulothrix zonata* first under the low and then under the high power. Draw a single cell showing the girdle-shaped *chloroplast* and its *pyrenoids*, and the *nucleus*. Hunt for stages of cell division and zoospore and gamete formation.

## C. SPIROGYRA

(7) Draw a single cell on a large scale under the high power showing *cell wall*, *cytoplasm*, *chloroplasts* and *pyrenoids*, *vacuole*, *nucleus* and *protoplasmic bridles*. A species with only one or two chloroplasts is easiest to draw in the first instance. Compare with a large species such as *Spirogyra crassa* containing seven or eight chloroplasts.

(8) Compare the *pyrenoids* of two preserved and decolorised samples, one of which has been well illuminated previous to killing and the other kept for a day or two in the dark. Stain each with iodine and observe again. Note that the pyrenoid itself stains brown (it is a protein) contrasting with the starch formed round it which stains dark blue or almost black.

(9) Examine the stages of conjugation of *Spirogyra*, fresh if possible, if not in preserved material and draw as many stages of the process as you can find.

## Chapter IX

### DIFFERENTIATION OF TISSUES FUCUS: THE SEA-WRACK

The Green Algæ are mostly unicellular or filamentous organisms such as those described in Chapters II and VIII, but some have a rather more elaborate construction. *Ulva lactuca*,<sup>1</sup> the "sea lettuce," forms a thin, crinkled sheet composed of two layers of green cells. More complex structure is met with in the two other large groups, the Red and Brown Algæ. They are also seaweeds and live mostly in the intertidal zone or just beyond the low-water mark. Their plastids contain chlorophyll but the greenness is masked by additional red and brown pigments. In the Brown Seaweeds there is a relatively small proportion of the green chlorophylls *a* and *b* and more of the yellow and orange xanthophyll and carotin. An additional pigment, resembling xanthophyll in its chemical structure, is also present. It is called *fucoxanthin*. Its addition to the more usual pigments results in an olive-green to brown colour in the plastids which are distinguished by the name of phæoplasts.<sup>2</sup>

The brown algæ vary from unicellular through a variety of filamentous forms to organisms with quite bulky bodies with more or less differentiated and specialised tissues. Some of the brown seaweeds, such as *Macrocystis*, and *Nereocystis*, living in the Antarctic and Pacific Oceans, are immense plants hundreds of feet long.

*Fucus*<sup>3</sup> is a genus of brown seaweeds of moderate size and wide distribution, which provides a convenient means of studying the fundamental principle of differentiation of function and corresponding differentiation of structure leading to the origin and development of distinct tissues. For this reason it repays a careful study.

Several different species of the genus live attached to rocks between tide marks of the north temperate zone. They are the commonest seaweeds of British coasts and festoon the rocks of the inter-

<sup>1</sup> Latin, lettuce.

<sup>2</sup> Greek φαίος (phaios), greyish.

<sup>3</sup> Latin *fucus*, reddish-purple.

tidal zone thickly. They are slippery and treacherous to walk on by reason of the copious mucilage spread on their surface.

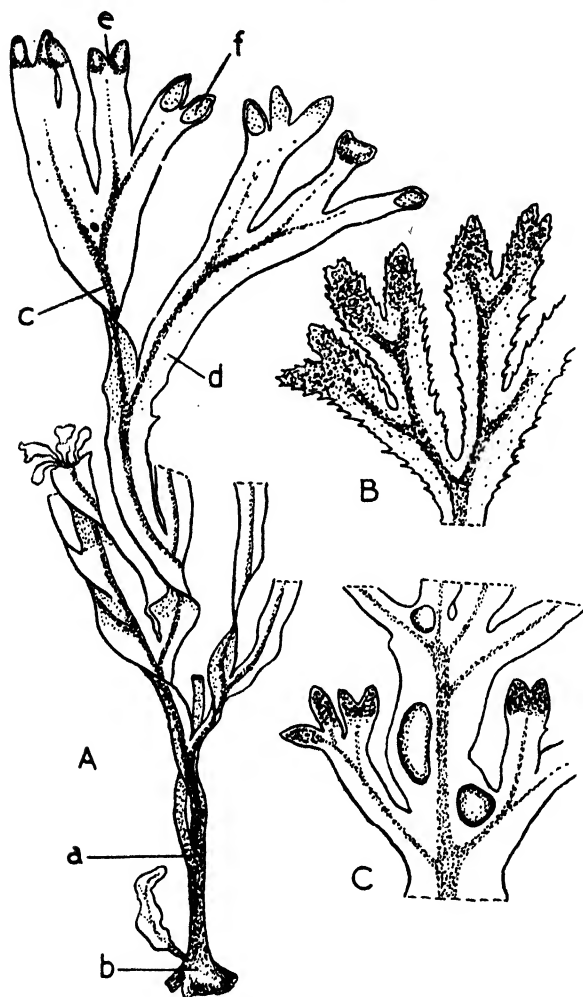


FIG. 61.—A, *Fucus spiralis*; a, stipe; b, holdfast; c, midrib; d, wing of frond; e, apical notch; f, conceptacles.  $\times 2/3$ . B, part of frond of *Fucus serratus* showing saw-like edges of the wings.  $\times 2/3$ . C, part of frond of *Fucus vesiculosus* with air bladders.  $\times 1$ .

Individual plants of *Fucus* vary from a few inches to over a foot in length. The body, or thallus (Fig. 61 A) consists of a cylindrical stalk, the stipe, which is attached firmly to the rock substratum by a



spreading holdfast. This is fixed extremely firmly to the rock surface by the glue-like mucilage that it produces; there is no penetration. Above, the stipe passes into the flat frond which branches repeatedly into equal halves. The midrib of the frond (Fig. 61 Ac) is a direct continuation of the stipe and on either side there are developed thinner wings. At the end of each branch there is a notch (Fig. 61 Ae) in which are situated the cells whose divisions cause the frond to grow.

The ends of some of the branches are swollen and show slightly raised papillæ, each of which is the projecting top of a hollow flask-shaped conceptacle. A minute hole leads through the tip of the papilla into the conceptacle which contains the sexual organs. There are also smaller, sterile conceptacles with hairs protruding through their openings.

*Fucus* thus shows an external differentiation of parts or organs. The holdfast fixes the plant below; the stipe has a tough strength which prevents the plant from being torn away from its base by the waves; the frond plays the chief part in photosynthesis; and the swollen frond tips are a localised reproductive zone.

#### *Microscopic Structure of the Thallus*

The minute structure of the different organs of bulky plants is best studied by examining under the microscope sections of the organ thin enough to be transparent when mounted in a liquid medium. To obtain complete information as to the structure of such an organ, these sections have to be cut in different directions. The most instructive section is that taken at right angles to the axis of symmetry of the organ (*transverse* or *cross section*), for this displays the distribution of tissues about that axis. But the knowledge gained from a transverse section must be supplemented by the examination of sections taken through and parallel with the axis (*longitudinal sections*), in order to study the structure of the tissues in longitudinal extension.

#### *Frond*

A cross-section of the middle of the frond shows three clearly marked regions: (a) the surface layer of cells (*palisade* or *photosynthetic* layer); (b) the larger isodiametric cells lying below (*cortex*); and (c) the central region of cells (*medulla*) the bodies of which are separated from one another by more than the thickness of an ordinary cell wall.

(a) *Palisade Layer*. This consists of a single layer of cells (Fig. 62 Ba) whose long axes are perpendicular to the surface of the frond.

Each cell of this layer essentially resembles a mesophyll cell (especially a palisade cell) of the leaf of a higher plant (Fig. 143, p. 226). It contains a central vacuole and a peripheral layer of cytoplasm containing the nucleus and packed with phæoplasts. In this layer (as in the palisade layer of the mesophyll of a typical leaf) the greater part

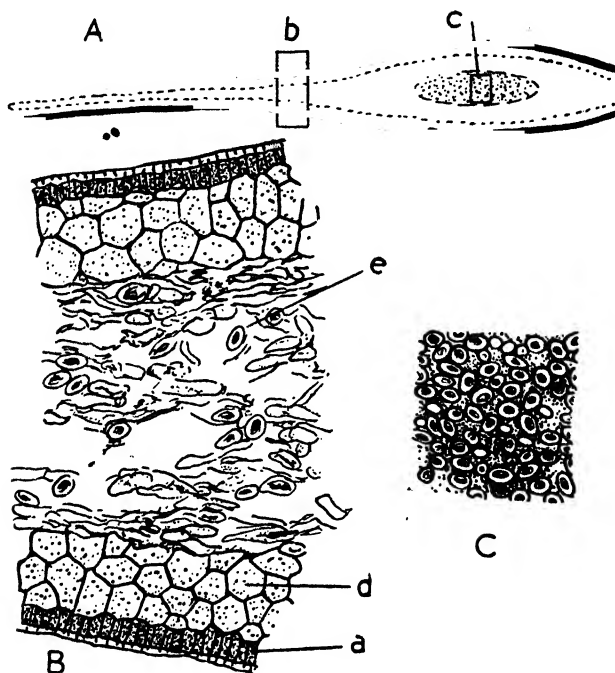


FIG. 62.—*Fucus* frond. A, diagram of transverse section of midrib and one wing. B, transverse section of part of the wing marked *b*, above; *a*, palisade with numerous phæoplasts and covered by a layer of mucilage; *d*, cortex; *e*, medulla consisting of chains of cells embedded in mucilage. The thick-walled ones are fibres. C, transverse section of part of midrib marked *c*, above and consisting almost wholly of fibres.  $\times$  about 250.

of the work of photosynthesis is carried on. These cells contain the greatest mass of phæoplasts and the raw materials of the process (water, dissolved carbon dioxide and mineral salts) have direct access to them when the plant is covered by the sea at high water.

(b) *Cortex*. These cells (Fig. 62 Bd) are larger than those of the palisade layer having larger vacuoles and fewer phæoplasts per unit bulk. The nucleus is often suspended in the vacuole by cytoplasmic bridges.

(c) *Medulla*. The central region of the frond is occupied by cells

(Fig. 62 Be) most of which are apparently isolated from one another. They are not, however, separated by air-spaces like the cells of many tissues of a higher plant, but by a mucilaginous substance which is really formed by the swelling of the middle layer of the joint

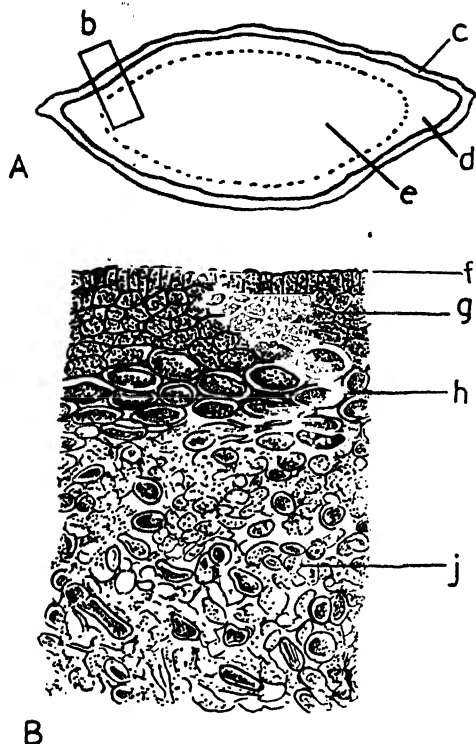


FIG. 63.—*Fucus*. A, diagram of transverse section of transition zone between frond and stipe; c, palisade; d, cortex; e, medulla. B, transverse section of part marked b above; f, palisade; g, cortex; h, fibres of outer layer of medulla; j, medulla.  $\times$  about 250.

wall between two adjacent cells. When these cells are first formed in development, the cell bodies are separated by thin walls, but the walls gradually increase in thickness and the middle layer becomes mucilaginous, takes up water and swells, forcing the cells apart and increasing the thickness of the thallus. The layers of wall on each side of this swollen middle layer, i.e. in direct contact with the cell bodies, also increase in thickness more or less, but remain of firmer consistency, so that in the adult condition the cells appear isolated, each covered by a wall of its own (which may be thin or thick) and separated from its neighbours by a muci-

laginous matrix. The medullary cells form chains or strands (like the threads of a filamentous alga) of cylindrical cells placed end to end. It is these chains that are separated from one another by the mucilaginous matrix derived from the middle layer of the original cell walls. The cross walls separating the successive cells of a medullary strand remain thin. The structure of the body of a medullary cell is not different in essentials from that of a cortical

cell, that is to say there is a central vacuole and peripheral cytoplasm with nucleus and phæoplasts, but these last are often very sparsely scattered.

The direction of the medullary strands differs in the wings and in the midrib. In the wings they run horizontally or obliquely; in the midrib longitudinally. In a cross-section of the thallus the strands are therefore lengthwise in the wings, but appear as circles in the midrib. Groups of cells at the outer edge of the medulla of the midrib, just below the cortex, have specially thick walls, and are called *fibres* (Fig. 63 Bb) by analogy with the somewhat similar cells of the higher plants. They serve like them to increase the toughness of the plant body; but do not have their lignification (p. 209) of the walls. The main function of the other medullary cells is probably the conduction of organic food substances, formed by the palisade, to the apical regions of growth.

In longitudinal sections of the frond the palisade and cortical cells appear very much the same as they do in transverse sections, but the medullary cells of the midrib look very different. They appear as elongated cells joined together in chains instead of as single cells cut transversely.

### *Stipe*

The stipe has no single layer of surface cells overlying a distinct cortex; but instead has radial rows of cells with thin walls which perform frequent tangential divisions parallel to the surface of the stipe. The surface itself is rough, owing to the fraying away of the outermost cells during the knocking about that the plant sustains from the waves. It often shows radial splits where rows of cells come apart. The medulla forms the greatest bulk of the stipe and has a much greater percentage of fibres than in the frond. It also includes a few wide cells having dense vacuolated contents with phæoplasts and fairly thick walls. These may perhaps conduct organic food from the frond to the holdfast, which keeps on growing. Towards the base of the stipe the fibres increase and the holdfast consists of nothing else.

### *Nutrition and Conduction*

The nutrition of *Fucus* is that typical of a green plant; but its chlorophyll is limited almost entirely to the surface layers. Photosynthesis is therefore limited to the outermost cells in contact with sea water, from which they obtain carbon dioxide and nutrient salts as well. All the cells of the bulky thallus respire and therefore consume sugars. The cells at the growing point probably consume

sugars and simple nitrogenous substances in synthesis much faster than they absorb them through their own restricted outer surfaces. It is therefore clear that food substances must pass from cells specialising in their formation to the consumer cells. The easiest channel for such a flow would appear to be through the strands of the

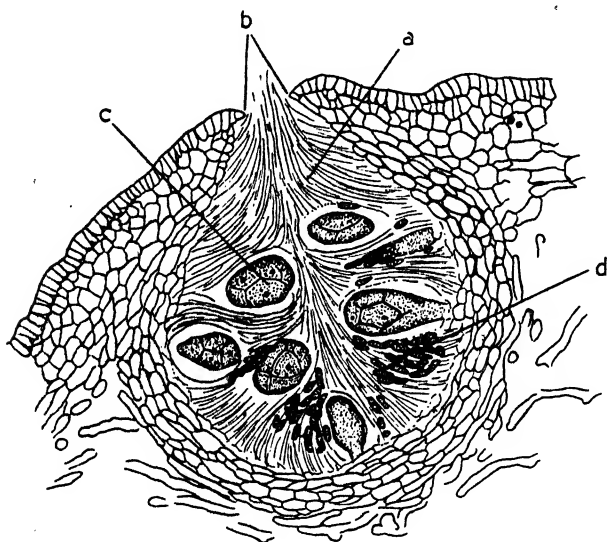


FIG. 64.—*Fucus spiralis* conceptacle. *a*, sterile hairs; *b*, pore; *c*, oogonium attached to conceptacle wall below the plane of the section; *d*, antheridia.  $\times$  about 250.

medulla, which provide the shortest path with the fewest obstructions. This is, however, largely a matter of inference, direct experimental evidence of such transport being hard to come by. It will be considered further in relation to the higher plants (p. 279).

### *Sexual Reproduction*

Unlike most of the plants so far considered, *Fucus* reproduces itself solely by means of gametes. It even differs from *Spirogyra* in this respect because its gametes show a high degree of sexual differentiation comparable with that of the gametes of *Volvox* (cf. Fig. 53, p. 110). The two kinds of gametes are produced in the cells of the sexual organs arising on the enclosed surfaces of the conceptacles. *Fucus spiralis* (Fig. 61 A) is monœcious with male and female organs in the same conceptacle (Fig. 64); *Fucus serratus*<sup>1</sup> (Fig. 61 B) and

<sup>1</sup> Referring to the saw-like edge of the frond.

*Fucus vesiculosus*<sup>1</sup> (Fig. 61 C) are dioecious, i.e. all the conceptacles of a given plant have sex organs of only one kind.

A conceptacle begins its development from a single surface cell which is still near to the apical cell of the frond and still within the apical notch. The initial cell (Fig. 65 A) becomes large and conspicuous and is divided by a cross wall into a tongue cell and a basal cell. At the same time, adjacent cells divide rapidly and push the tongue and basal cells downwards to the bottom of the developing cavity (Fig. 65 B). The basal cell divides repeatedly, first by vertical and then by cross walls to form the bottom of the conceptacle (Fig.

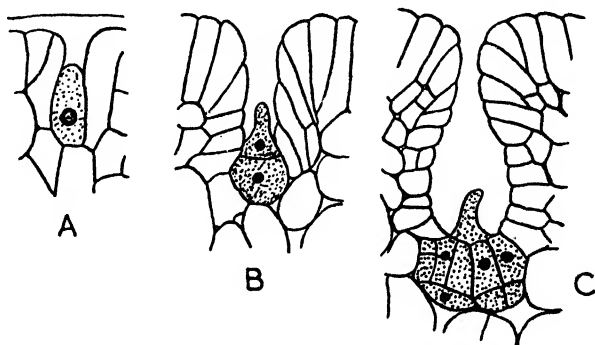


FIG. 65.—*Fucus serratus*, development of a conceptacle. A, initial cell. B, tongue cell above and basal cell below. C, divisions forming bottom and sides of the conceptacle. After Nienburg.

65 C); the sides are formed by the adjacent cells. The female organs, the oogonia,<sup>2</sup> each arise from a single cell on the wall of the conceptacle. This grows up to form a papilla which is cut off by a cross wall at the base and then divides transversely to form a stalk cell and a body cell (Fig. 66 A). The latter becomes large and spherical and its nucleus divides into eight by successive bipartitions. The first two of these comprise the reduction division, and then there is a pause before the third division occurs to give the complete set of eight nuclei. The cytoplasm divides correspondingly and forms eight eggs which are separated by fine membranes connecting with the innermost layer of the oogonium wall (Fig. 66 B) which forms three layers in all. When the oogonium is ripe the outermost layer bursts, setting free the eggs in a bladder composed of the middle and inner layers of the wall.

<sup>1</sup> Having bladders dispersed about the thallus.

<sup>2</sup> Greek ᾠόν (ōon), egg, and γόνος (gonos), offspring.

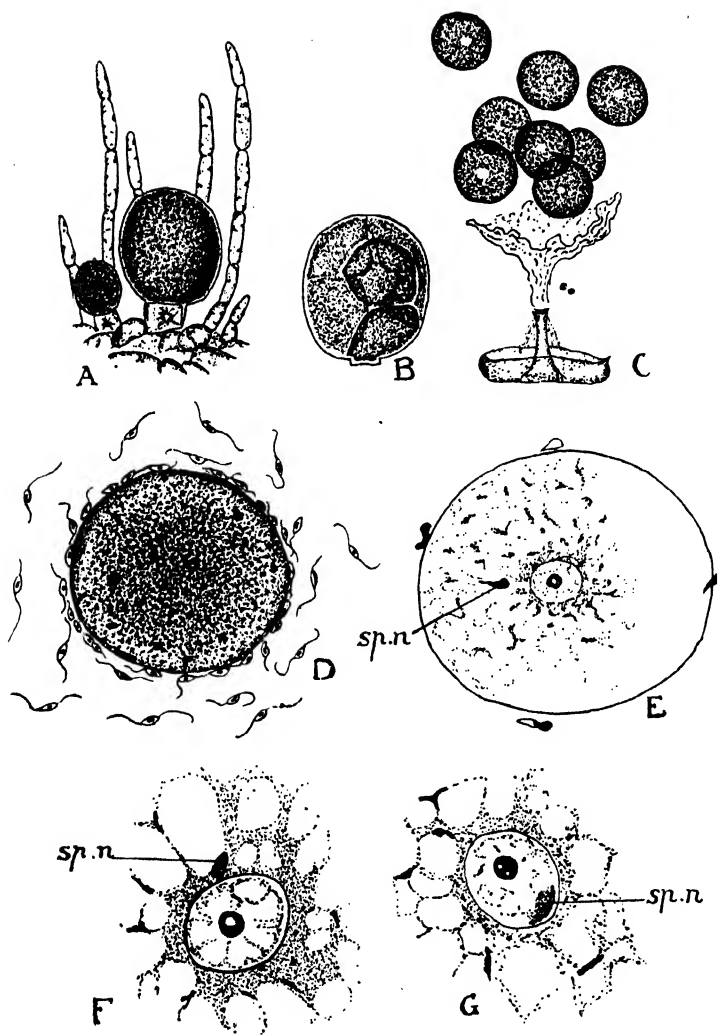


FIG. 66.—A, oögonia developing from wall of a conceptacle, body cell above and stalk cell below. B, body cell of oögonium containing eight young eggs. C, eggs escaping after the breakdown of the inner layer of the oögonial wall. D, single egg surrounded by sperms. E, egg penetrated by sperm; *sp.n.*, sperm nucleus. F, sperm nucleus in contact with egg nucleus. G, sperm nucleus fused with egg nucleus.

The male organs, the antheridia, are club-shaped cells (Fig. 67 A) forming branches of a hair that arises, like the oogonium, from a surface cell of the conceptacle. The nucleus of the antheridial cell divides repeatedly to form sixty-four nuclei; the first division being

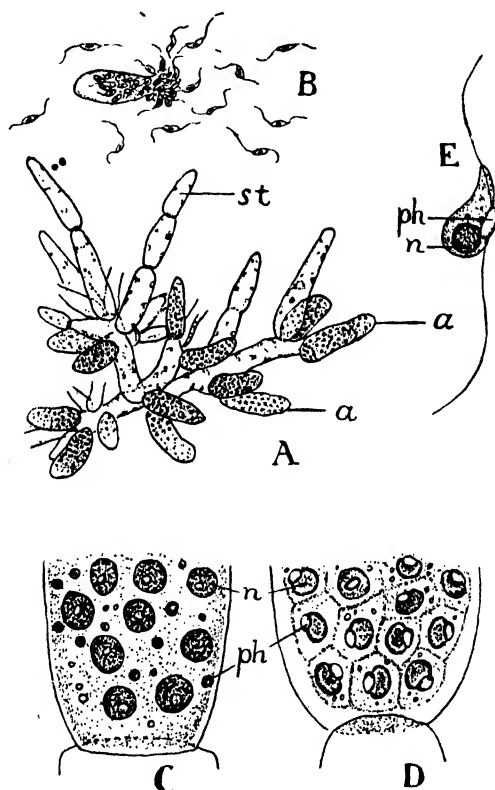


FIG. 67.—A, branched hair from a conceptacle showing *a*, antheridia and *st*, sterile cells. B, sperms escaping from the bladder formed by inner wall of an antheridium. C and D, sperms developing inside an antheridium; *n*, sperm nucleus; *ph*, sperm phaeoplast. E, free sperm with two flagella attached at one side.

meiotic, as in the development of the oogonium. The cytoplasm divides correspondingly and sixty-four sperms are thus formed. Each is a minute biflagellate, pear-shaped cell containing, besides the nucleus (Fig. 67 E), a single orange phaeoplast. The antheridial wall has two layers when mature and the mass of sixty-four sperms escapes from the antheridial hair enclosed in the inner layer.

Besides oogonia and antheridia the conceptacles always contain



numerous sterile hairs (Fig. 64) arising from their walls. Those near the fine opening project through it as a tuft to the outside. The cavity of the conceptacle is filled with mucilage, probably produced by some of the included hairs. The pressure of the developing hairs and the mucilage forces the bladders containing the eggs and the sperms out through the pore. This occurs at low tide, but may also happen when the plant is submerged. The masses of sperm bladders, where these are extruded from different conceptacles from the eggs, can easily be distinguished with the naked eye by their bright orange

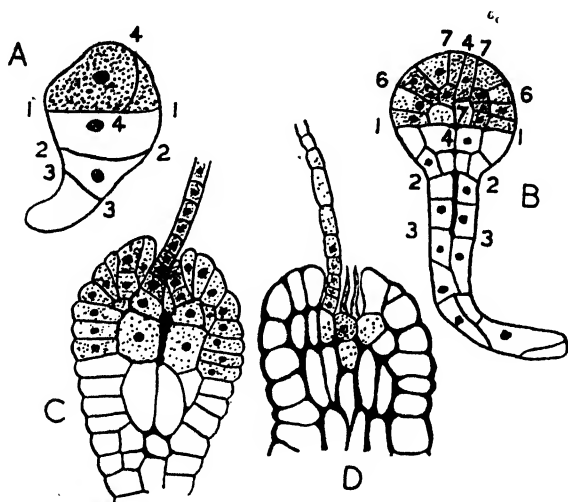


FIG. 68.—*Fucus vesiculosus*, development of the young plant. A, embryo showing young rhizoid and body cells. The numbers against the walls indicate the order of the cell divisions. B, after further divisions. C and D, development of the apical notch. After Nienburg.

colour due to the orange phaeoplasts of the sperms. In sea water, the middle, now the outside, layer of the oogonial wall becomes gelatinous. It develops a pore at the apex and rolls back (Fig. 66 C). The inner layer of the wall then dissolves and the eggs are set free. The sperms are similarly released by the breakdown of the inner layer of the antheridial wall.

The spherical egg contains much food material and is many times the diameter of the sperm. It secretes a substance of unknown composition which attracts the sperm. The sperms are said to react negatively to air and light and positively to gravity. They thus tend to follow the heavy eggs which are apt to sink to the bottom. An egg is liable to be surrounded by many sperms which become attached

by one of their flagella. The activity of the free flagella sets up a vortex in which the egg rotates (Fig. 66 D). One of the sperms penetrates into the cytoplasm of the egg and the formation of attractive substances then ceases. The male nucleus passes rapidly towards the female and fuses with it (Fig. 66 F and G). Though the sperm nucleus is much smaller than that of the egg, the number of chromosomes and the amount of hereditary material it contains is always the same (cf. p. 148).

### *Development of the Young Plant*

The fertilised egg does not form a resting zygote, as in the simpler algæ described in Chapter VIII, but germinates at once. A cell wall

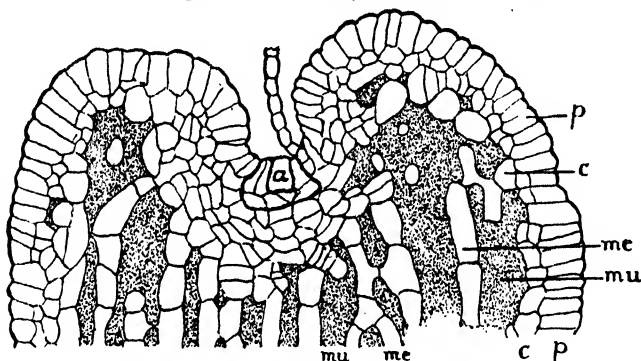


FIG. 69.—Longitudinal section of young apex of *Fucus* in the plane of the wide axis of the frond; *a*, apical cell; *c*, cortex; *me*, medulla; *mu*, mucilage of the medulla (shaded); *p*, palisade.

is secreted and the side away from the light lengthens and becomes pointed. The cell divides and forms a cross wall (Fig. 68 A); the daughter cell at the pointed end forms the first attaching organ, or rhizoid,<sup>1</sup> which sticks to any solid substratum with the help of its mucilaginous wall. It probably does no absorption. The upper cell divides repeatedly, first by a vertical wall (Fig. 68 A) and then builds up a club-shaped body (Fig. 68 B). At the same time fresh rhizoids grow out at the base. Very soon one or two hairs are formed at the apex (Fig. 68 C). The surrounding cells separate at their base (Fig. 68 D) and so form the apical depression in the bottom of which lies the apical cell that is responsible for the subsequent growth of the frond (see p. 126). This is at first triangular in cross-section but later becomes four-sided (Fig. 69). The depression becomes more marked owing to the rapid growth and division of the surrounding surface

<sup>1</sup> Root-like organ. Greek *ρίζα* (rhiza), root.

cells. Up to this point the young plant has been nearly cylindrical but now the upper part grows quickly in a single longitudinal plane and thus the wings of the frond are started.

A marked difference is soon apparent between the growth of the surface cells and those occupying the centre of the thallus. The former remain small, but divide frequently and form the palisade layer (Fig. 69 p). The cells lying immediately below do not divide so rapidly, but tend to become larger (Fig. 69 c). They form the cortex. The central cells (Fig. 69 me) are still more sluggish and become passively stretched in the longitudinal direction as the surface layer increases by active growth and cell division. At the same time the middle layers of the walls of these medullary cells become mucilaginous and separate them from one another laterally, thus giving rise to the characteristic structure of the medulla. The chains of thick-walled "fibre" cells in the holdfast, the medulla of the stipe and the midribs of the fronds, begin to grow out from the cortical and medullary cells as soon as they differentiate. They form hyphæ that grow independently in the mucilaginous matrix.

The same contrast between outer and inner cells can also be seen in other Brown Seaweeds not at all closely allied with *Fucus*, whose thallus consists of stout cylindrical threads from six to twenty cells thick. The surface cells are small and densely filled with phæoplasts, the central cells are larger and, especially, longer and possess many fewer phæoplasts per unit volume. Indeed, the same distinction occurs to some extent in the tissues of most of the highly organised plants (see, for example, young roots, p. 247) and is referable to the different rates of cell growth and division in the different tissues. The determination of the different growth rates is complex and depends on nutrition, hormone control (cf. p. 284) and other obscure influences.

### *Adaptation to the Intertidal Zone*

Although *Fucus* is a relatively simple plant of lowly status in the plant kingdom, it is very closely adjusted to the special conditions of its unusual environment. Its organisation provides a very efficient response to the special requirements, and it can perhaps be regarded as fully evolved under the circumstances of its existence. The special characters of its environment are the often violent wave action and frequent variation from submerged to exposed. The first makes it impossible for any free-floating or unicellular algæ to inhabit the zone—they would simply be swept away. *Fucus* resists this by the

gumming of its holdfast to the rocks, by the leathery, non-brittle toughness of its stipe and fronds, and by its relatively simple form which is not readily torn to shreds. It escapes drying out when exposed by means of the moisture-retaining mucilages secreted over its surface, which also afford a medium for fertilisation without complete dispersal of the sperms. When submerged it is able to absorb nutrients all over its surface so that the rudimentary conducting tissues it possesses are probably adequate for what is needed; the air-bladders present in some forms help flotation and spreading of the thallus. It is possible that the brown colour is also a sort of chromatic adaptation increasing the absorption of blue light which penetrates into water more effectively than yellow or red.

## Practical Work

### FUCUS

#### *Vegetative Structure*

(1) Make a sketch of samples of the *thallus* of *Fucus* showing the *holdfast*, the *stipe*, the *branching*, the positions of the *apical grooves* and the *conceptacles*. Note that the stipe is extremely tough and cannot be broken by pulling with the hands, whereas the frond can. If the frond is broken the hair-like *fibres* may be seen projecting from the broken surfaces.

(2) Examine a cross-section of the *frond* under the low power, and draw a *diagram* of the general plan of distribution of the tissues, marking:

(a) The *palisade* (*photosynthetic*) layer on the surface.

(b) The *cortex* of large isodiametric cells with fewer *phæoplasts* per unit volume.

(c) The *medulla* of elongated cells running in strands in various directions, and separated by a matrix of cell-wall substance.

Note that the extra thickness of the *midrib* is caused by the greater thickness of the medulla in that region.

(3) Examine a cross-section of the *frond* under the high power and make careful *drawings* of small samples of the various tissues, including the thick-walled *fibres* ("hyphæ") which are mainly localised just below the cortex of the midrib on the edge of the medulla. Note that the conducting cells run horizontally or obliquely in the wings, and longitudinally (so that they are cut transversely) in the midrib.

(4) Examine two longitudinal sections of the *frond* (a) cut through the midrib at right angles to the surface of the frond; (b) cut parallel to the surface of the frond through the centre. Identify the various tissues already seen in transverse section, and, from a comparison of the appearance of the cells in the two views, deduce their shapes. Draw under the high power samples of the cells which are not identical in appearance in transverse and longitudinal sections. Note the thin transverse walls of the conducting cells.

(5) Examine transverse and longitudinal sections of the *stipe*, noting the differences between its structure and that of the frond, especially (a) the *worn surface* with radial splits between the surface cells; (b) the absence of a distinct palisade layer and the radial rows of *cortical cells* with relatively thin tangential walls, indicating that this layer has been largely formed by secondary cell division parallel to the surface; (c) the mass of *fibres* ("hyphæ") mostly cut transversely,

forming the *medulla*, interspersed with large isolated cells (the original medullary cells). Make drawings to illustrate these points. In the longitudinal section of the stipe identify the tissues seen in transverse section.

(6) Examine a longitudinal section through the *apex* of the frond showing the *apical cell* and the origin of the adult tissues.

#### *Sexual Organs*

(7) Examine a section across the *reproductive region* of the thallus first under the low power. Note that the vegetative tissues have the same general characters as in the purely vegetative part of the frond, but that the medullary cells here form a network, the cells being cut in various directions. This is the result of the increase in thickness of this part of the frond, the strands of cells being drawn out in all directions, not only in one direction.

(8) Examine the development and structure of the *antheridia* and *oogonia* in the same or in different *conceptacles*, and draw as many stages of development as you can distinguish. Note also the *sterile hairs* in the conceptacle.

(9) Examine fresh material in which *eggs* and *sperms* have been liberated and appear as little masses on the outside of the frond. In species with the sexes on separate plants the sperms can be distinguished by their bright orange colour. Mix some eggs and sperms in a drop of sea-water or in salt solution of about the same concentration. Draw under the high power an egg and some sperms and watch the movements of the latter. The early stages of fertilisation (conjugation) can often be seen.

## Chapter X

### THE SIMPLEST LAND PLANTS : PELLIA

#### *The Aquatic Ancestry of Land Plants*

The plants described in the preceding chapters nearly all live in water. They are simple and primitive types. They may be perfectly fitted to their submerged existence and are at least reasonably well suited or they would not continue to exist (cf. p. 338). Except for a few degenerates, plants of a high degree of organisation are not found growing under water. The more complex types are land plants rooted in the soil and freely exposed to air. Their environment is heterogeneous and variable to a degree quite unmatched in a pond or in a tract of ocean. The elaborate structures and organisation of the higher plants may be regarded as adaptations called forth by the greater demands of their position. Nevertheless it is clear that even the most highly developed land plants had an origin in the water. Through the ages of geological history a colonising "migration" occurred; just as plant migrations, accompanied by gradual changes in the migrating plant generations, are manifestly pursuing their slow courses around us to-day.

Nothing is known of how the first emergence of plants from the water took place; nor does it seem very likely that such knowledge can be gained. The subsequent evolution of the higher land plants may, however, be regarded as an increasing adjustment to terrestrial and subaerial conditions. However far this has gone, even in the flowering plants the most highly adapted of all, evident marks of an aquatic ancestry remain. In no other way can their make-up be grasped or their nature be understood. Land plants have not arisen with a clean slate, as it were, in sole response to the needs of their existing milieu; but as adaptations, a "making do" from something previously existing.

Two great themes run as a result through the history of the land plants, one affecting the germ cells and the other the soma. The first of these fundamentals is due to the dependence of all free-

swimming gametes upon water for their coming together, and crystallises in the alternation of generations (Chapter XI) characteristic of all higher plants. The second results from the fact that all living cells are about 90 per cent. water. The soma exposed to a desiccating atmosphere must have powers of protection, retention or absorption unneeded by a submerged one, or must be able to endure periods of drying out without destruction. The structures and capabilities of the higher plants all have their existence within the limits set by these restrictions.

Land plants of all degrees of adaptation to subaerial conditions exist at the present time. Although many are much simpler than the flowering plants it would obviously be an absurdity to think of them as their ancestors. It is not even very likely that they resemble at

all closely those long-vanished forms. The existing simple plants have perhaps become stabilised at an early stage of adjustment and usually inhabit situations where water is still abundant at least at some seasons. They have found their niche and survive.

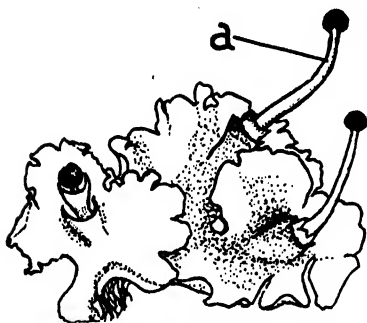


FIG. 70.—*Pellia*, thallus. *a*, sporogonium. Nat. size.

#### PELLIA

*Pellia* is a genus of liverworts which provides a convenient example of a simple land plant

capable of existing only in a moist situation. It is found growing on the ground among damp herbage or in marshes. Its body is a thallus, that is to say it has no external differentiation of its form into special organs, but consists simply of a flat green tissue which may be strap-shaped or may divide repeatedly into equal halves to form a tuft of short branches. The margins of the thallus are often crisped because they have grown faster than the somewhat thicker central part and so have been thrown into folds (Fig. 70). The lower surface bears long cellular outgrowths, the *rhizoids*, which enter the soil and absorb water and salts from it. Absorption of water probably goes on to some extent all over the moist surface of the thallus.

#### *Structure of the Thallus*

The thallus consists entirely of thin-walled living cells with chloroplasts which are most numerous in cells near the surface (Fig. 71).

These cells may also have starch grains in their chloroplasts if recently illuminated. There is little differentiation in the structure of the cells, but those in the thicker central portion may be slightly elongated in the direction of the long axis of the frond. The central cells also have large "storage" starch grains, bursting their chloroplasts, which remain as green adhesions to the surface (cf. Exp. (6), p. 70). The rhizoids are outgrowths from surface cells of the central region. The thallus of *Pellia* is thus of very simple construction; its surface layers and its midrib, while showing slight differentiation in the direction of photosynthesising, conducting and storing tissues

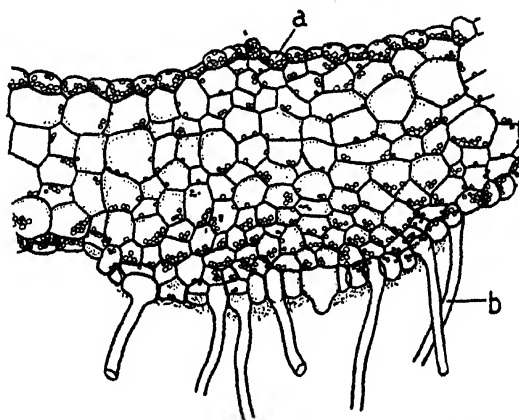


FIG. 71.—*Pellia*, vertical section of thallus. *a*, cells of the upper surface with numerous chloroplasts; *b*, rhizoids.  $\times$  about 100.

respectively, fall far short of that achieved by *Fucus*. On the other hand, the rhizoids represent a rudimentary differentiation of an absorbing tissue which is absent from *Fucus* entirely.

*The Growth of the Thallus* is apical and is due, as in *Fucus*, to the divisions of a single apical cell, which may be situated in an apical notch. Daughter cells are cut off from two or four sides, and each daughter divides into five or six more before the apical cell itself divides again. In this way the whole of the tissue of the thallus is slowly built up.

### *Reproduction*

The thallus of *Pellia* produces sexually differentiated gametes. In this it resembles *Fucus* and all the higher land plants. A further point of resemblance with *Fucus* is that the gametes are formed in sexual



organs arising from surface cells of the thallus. The sex organs of *Pellia* are more developed, however, and have a wall consisting of a

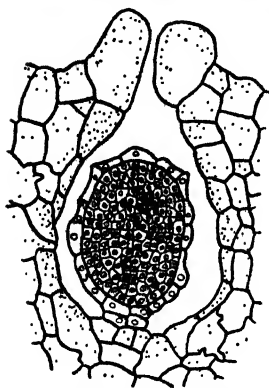


FIG. 72.—*Pellia neesiana*, vertical section of antheridium and surrounding tissue of the thallus.  $\times 160$ . After Smith.

layer of cells instead of only the wall of the original cells forming them. Male organs, the antheridia, and female, the archegonia, may be produced on the same or only on different thalli. If on the same thallus, the antheridia appear first and are irregularly scattered along the upper surface of the midrib. Each antheridium lies in a little cavity formed by thallus tissue growing up and round its flanks (Fig. 72). The antheridium develops first by two successive divisions of a surface cell parallel with the surface of the thallus (Fig. 73 A), and then periclinally to form the jacket cells (Fig. 73 C). The inner cells then divide repeatedly to form the sperms (male gametes), while the outer cells keep

pace with frequent divisions to form an antheridial wall one cell thick (Fig. 73 G). The mature sperms are long, narrow spirals with

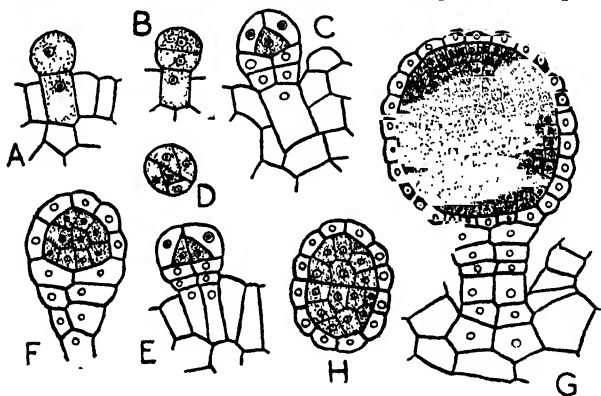


FIG. 73.—Stages in the development of the antheridium of *Fossombronia angulosa*, closely allied to *Pellia*. A, surface cell dividing. B, first division of antheridial cell. C, periclinal divisions forming wall. D, the same in transverse section. E and F, further divisions to form stalk and sperms. G, mature antheridium. H, the same, earlier, in transverse section.  $\times 210$ . After Smith.

two flagella inserted near to one another at the anterior end (Fig. 74 A). They are somewhat like the sperms of *Volvox* (p. 110) but have no chloroplast and only a trace of cytoplasm where the flagella

are attached. They are therefore even further whittled down to essentials than the sperms of *Volvox* and *Fucus*. They consist almost solely of the paternal hereditary material in the nucleus and

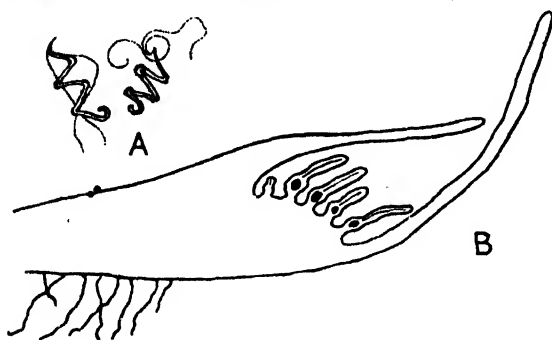


FIG. 74.—*Pellia*. A, sperms, after Thuret. B, diagram of thallus showing archegonia and the involucre covering them.

the means of getting it to the female. They have no means of nutrition of their own or reserves to fall back upon; once they are released fertilisation must occur soon or fail.

The archegonia<sup>1</sup> are formed near the apical cell on a cushion of

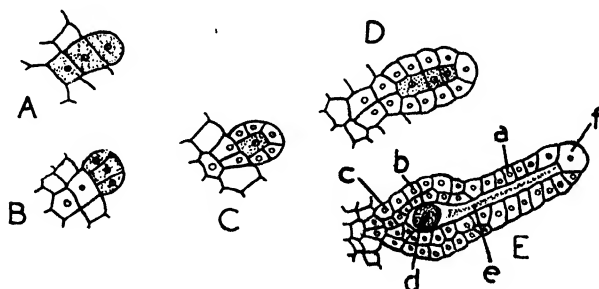


FIG. 75.—Development of the archegonium of *Fossombronia angulosa*. A, divisions of a surface cell of the receptacle. B, vertical divisions of the archegonial cell. C and D, formation of wall and stalk cells. E, archegonium ready for fertilisation; a, neck; b, venter; c, stalk; d, egg; e, mucilage; f, cap cell which is forced aside by pressure of the swelling mucilage. A–D  $\times 210$ ; E  $\times 150$ . After Smith.

tissue called the receptacle. Any surface cell of the receptacle may develop into an archegonium and usually a number do so, one after the other in a slow succession (Fig. 74 B). They are overhung by a membrane which grows out from the thallus behind them. The com-

<sup>1</sup> Greek ἀρχή (archē), first, beginning and γονή (gonē), womb.

pleted archegonium is a flask-shaped organ consisting of a neck and venter<sup>1</sup> raised on a short stalk (Fig. 75). There is a single relatively large egg enclosed in the venter, which it practically fills. The neck is filled with mucilage formed by the breakdown of an internal row of cells. The wall of the neck is built of five rows of cells and remains one cell thick. At the venter the cells may divide periclinally and the wall becomes two cells thick as a result (Fig. 75 E b).

**Fertilisation.** When the surface of the thallus is sufficiently moist with rain or dew, the ripe archegonium bursts open at the tip of the neck. Sperms are released from the antheridia by the separation of

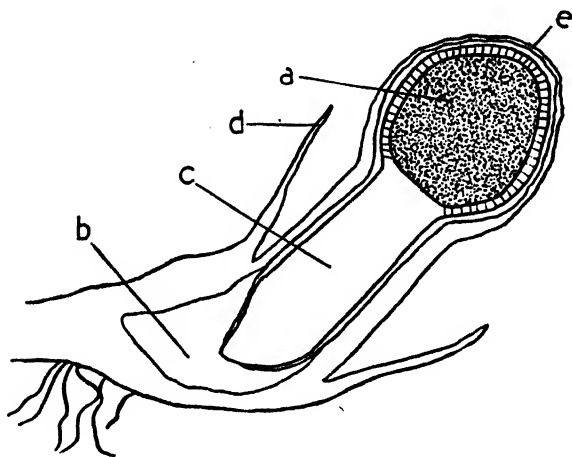


FIG. 76.—Diagram of a young sporogonium of *Pellia*. *a*, spore capsule; *b*, foot; *c*, stalk not fully elongated; *d*, involucre of the thallus; *e*, remains of the archegonial wall.  $\times 11$ .

cells near the top of the wall, which folds back leaving the mass of sperms exposed. They emerge in a cloud into the overlying film of water in which they swim freely. They are attracted to the archegonia by the excretion of specific compounds, which have not been identified in *Pellia*, but which are known to include soluble proteins and salts of potassium in some other liverworts. At the mouth of the archegonia the sperms enter the mucilage and wriggle down the neck until one fuses with the egg and so forms the zygote, which at once secretes a wall and begins to germinate after only a few days' delay.

The egg and zygote of *Pellia* are smaller than those of *Fucus*. They are not cast out of the thallus, but remain *in situ* during fertilisation and their subsequent development. The young embryo is, therefore,

<sup>1</sup> Latin, belly.

not solely dependent upon food reserves in the cytoplasm of the egg, but is further nourished from the thallus itself. This is our first example of the feeding and protection of the embryo by the mother organism. It is a development obviously of great importance and is carried to much greater lengths both in the higher plants and higher animals.

### *Sporogonium*

The embryo of *Pellia* does not develop directly into another thallus but into a special structure, the sporogonium, that remains

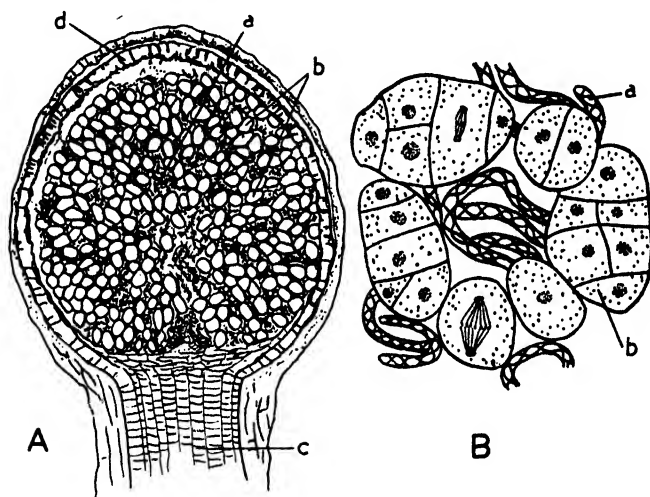


FIG. 77.—A, ripe capsule with *a*, elaters and *b*, spores; *c*, stalk and *d*, wall.  $\times 30$ . B, components further enlarged; *a*, elaters; *b*, spores dividing while still in the capsule.  $\times$  about 350. After Smith.

attached throughout its life to the parent thallus (Fig. 76). It produces spores which in their turn germinate to form new thalli.

The mature sporogonium consists of a foot, embedded in the thallus and drawing nourishment from it, a long stalk, and a spherical spore capsule (Fig. 76). The wall of the capsule is several cell-layers thick and contains a mass of spores which divide to a 6 to 9-celled stage while still enclosed in the capsule (Fig. 77). The capsule becomes dark coloured, almost black, and opens in dry air by four splits running from the top almost to the stalk at the bottom. The wall folds back in four flaps and the mass of spores is exposed. As the sporogonium matures some of the sporogenous

tissue develops into long cells with spiral thickenings inside their walls. These are called elaters.<sup>1</sup> Similar cells remain attached to the base of the spore capsule and entangle some of the spores. The spores are shed as a young 6 to 9-celled thallus which immediately resumes growth on moist soil. The basal end sends out a rhizoid and, at the opposite anterior end, a definite apical cell responsible for the growth of the thallus soon arises.

The sporogonium begins with one reproductive phase, the fertilised egg, and ends with another, the spore. It is thus a complete plant generation, but it never attains independent existence, remaining a dependant of the thallus all its life. The two generations succeed one another in a fixed and obligate alternation, a state of affairs which persists throughout the whole series of the higher plants. Its importance and implications will be considered more fully in the next chapter.

#### LIVERWORTS AND MOSSES<sup>2</sup>

*Pellia* is an example of a simple thalloid liverwort. It has numerous allies with similar simple constructions and life histories. There is also a group of "leafy liverworts" whose shoots have distinct "stems" and "leaves." These names are perhaps a little misleading since in spite of the external differences there is very little internal differentiation of tissues. The "leaves" consist of a single cell layer of chlorophyll-bearing cells and the "stems" of rather similar cells a little elongated. Water is absorbed all over the surface and rhizoids are also formed which attach the plant to the moist surface on which it is growing.

The mosses resemble the liverworts in many respects but are more bulky and a little more elaborated in most respects. They always have stems and leaves with sometimes a little more differentiation of tissues than the liverworts. Elongated cells which have lost their contents appear to act in the stems as definite conductors of water upwards from the soil. Their rhizoids are branched multicellular growths from the base of the stem. The leaves may have a midrib, several cells thick, including thin-walled water-conducting cells. The shoot grows by means of an apical cell similar to that of *Fucus* and *Pellia*.

The soma of the mosses is rather better adapted to existence on land than the soma of the liverworts. Some mosses have been able to

<sup>1</sup> Latin, *effere, elatum*, to bring out. A reference to a rather doubtful effect of these cells.

<sup>2</sup> See also p. 12.

colonise dry habitats such as roofs and exposed rocks by a property which is not a result of either their gross or their microscopic structure. Their protoplasm is capable of resuming active life when it is moistened after a period of drastic drying-up such as would kill other unprotected protoplasts.

Though they can absorb water all over their surfaces, many of the mosses have a regular water current from rhizoids to leaves. They have a water-conducting tissue corresponding with the localisation of absorption in one part of the body and its evaporation in another. This feature is carried to much higher levels of development in the vascular plants. Another feature of vascular plants, the conduction of food materials, present in the bulky thallus of *Fucus*, is not in evidence in the smaller bodies of either the liverworts or the mosses.

On the side of the germ tissue, the mosses show no important differences from the liverworts in their sexual reproduction; but the asexual reproduction by spores is furthered by elaborations of the sporogonium.

## Practical Work

### PELLIA

(1) Examine plants of *Pellia*. Sketch the form of the *thallus*. Note the crisped edges, the *midrib* with *rhizoids* and the thin *wings* at the side.

(2) Mount a transverse section of the *thallus* in dilute glycerine and examine under the microscope. Note the almost uniform thin-walled tissue. The *chloroplasts* are usually most numerous towards the upper surface but sometimes also towards the lower. Examine them for *starch grains*. Note the *rhizoids* coming from the lower surface of the midrib. Make an outline diagram, using the low power, and a detailed drawing of sample cells from the upper and lower surfaces and centre.

(3) Open a ripe *spore capsule* and *tease* out some of the contents into a drop of dilute glycerine. Examine and draw the *elaters* and the young *multicellular thalli* already developed from the *spores*. Note the *chloroplasts*.

(4) Make a low-power diagram of a prepared longitudinal section of a *sporogonium* showing *stalk*, *capsule*, *spores* and *elaters*.

### MOSSES

(5) Make a sketch of a single plant of a moss, e.g. *Funaria* or *Polytrichum*, using a hand lens. Note the *axis* (stem), *rhizoids*, *leaves*, *stalk*, and *spore capsule*.

(6) Immerse a moss-leaf in M/2 sucrose or M/5 calcium chloride. After a quarter of an hour, mount in the same medium and examine under the microscope. Instead of plasmolysing, the cells may be thrown into folds because their *walls* are often semipermeable; or they may be permeable only in places, so that plasmolysis develops locally.

(7) Examine a prepared transverse section of a *moss stem* showing the *outer cortex* of thick-walled cells, the inner *cortex* of thin-walled cells and the *central strand* of narrow, thin-walled water-conducting cells.

## Chapter XI

### ALTERNATION OF GENERATIONS DRYOPTERIS

#### *Zygosis<sup>1</sup> and Meiosis<sup>2</sup>*

The specialisation of the male gamete involves its reduction from a more or less normal, free-swimming cell, such as it still is in *Chlamydomonas braunii* (p. 102), to little more than a flagellated nucleus as in *Pellia*. Whatever lengths reduction goes to, the hereditary material remains complete and there are just as many chromosomes in the tiny sperm as in the relatively large egg. It follows that every time a sexual fusion takes place the chromosome complement of the fused cell is doubled. This, by itself, would lead in a few plant generations to an impossible state of affairs which does not, in fact, occur. The chromosome number remains constant for any particular species, and is one of its most reliable characteristics. It is evident, therefore, that *zygosis*, the doubling of the chromosome number, must be followed at some stage of the life history by a corresponding reduction or *meiosis*. This is brought about when two cell divisions are accompanied by only one separation of chromosomes (p. 332). As a result, a single mother cell divides into a *tetrad* of four daughter cells, each of which has half the number of chromosomes possessed by the mother cell. The nuclear details of this process are of great importance in the study of heredity and will be described more fully in Chapter XXV.

The precise point of the life history at which meiosis occurs varies in different species. In *Spirogyra* it is upon the earliest possible occasion, and the zygote divides to form a tetrad while still within its own thick wall. Three of the resulting nuclei degenerate before any new walls are formed and, when germination occurs, the cells of the new filament have the same chromosome equipment as those of the parent filaments (Fig. 60, p. 120). *Fucus*, on the other hand, delays the reduction until the last possible moment, i.e. when new

<sup>1</sup> Greek, the yoking of a pair.

<sup>2</sup> Greek, reduction, making less.

gametes are about to be formed. Meiosis occurs in the first two divisions of the antheridia and archegonia. Algæ, such as *Volvox* and *Ulothrix*, form asexual spores and zygotes without any definite succession. Meiosis occurs, as in *Spirogyra*, at the first division of the zygote and an increased number of chromosomes is present only in the zygote itself.

<i>Plant</i>	<i>Meiosis occurs at</i>	<i>2n chromosomes present in</i>
<i>Volvox</i> (p. 111) . . .	First divisions of zygote.	Zygote only.
<i>Spirogyra</i> (p. 118) . . .	First divisions of zygote.	Zygote only.
<i>Ulothrix</i> (p. 115) . . .	First divisions of zygote.	Zygote only.
<i>Fucus</i> (p. 133). . . .	First divisions of the antheridium and archegonium.	Zygote and plant.
<i>Dictyota</i> (p. 149) . . .	Formation of spore tetrads from spore mother cells.	Zygote and sporophyte.
<i>Dryopteris</i> (p. 154). . .	Formation of spore tetrads from spore mother cells.	Zygote and sporophyte.
<i>Selaginella</i> (p. 164). . .	Formation of micro- and mega-spore tetrads from mother cells.	Zygote and sporophyte.
<i>Pinus</i> (p. 170) . . . .	Formation of micro- and mega-spore tetrads from mother cells.	Zygote and sporophyte.
Flowering plants (p. 300)	Formation of micro- and mega-spore tetrads from mother cells.	Zygote and sporophyte.

### *Alternation of Generations*

In the land plants a strict alternation of zygote and spore formation is maintained. This also appears in some of the more highly organised brown seaweeds, such as *Dictyota*, and the large kelps (*Laminaria*), and in red seaweeds such as *Polysiphonia*. A regular cycle, or alternation of generations, is thus set up in which meiosis invariably occurs during spore formation. Sooner or later, during the development of the sporogenous tissue inside the sporangium, spore mother cells are formed which perform a double cell division, yielding a tetrad of four spores, each with the reduced chromosome number. This process is essentially similar in all plants from the

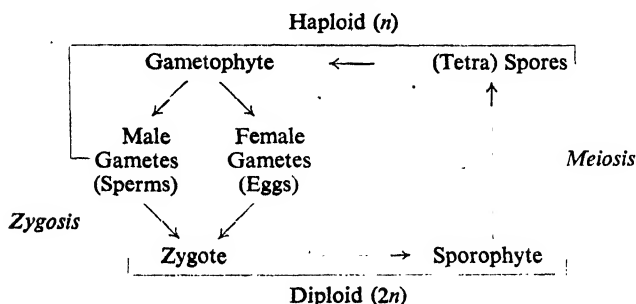


higher seaweeds (Fig. 78) to the flowering plants. It results in the existence of two distinct generations of each species.

(a) *Gametophyte*. The gametophyte is produced by the germination of the spore and itself produces gametes—sperms and eggs. It is *haploid*<sup>1</sup> that is to say all its cells possess the reduced ( $n$ ) number of chromosomes.

(b) *Sporophyte*.—The sporophyte is formed by the germinating zygote and terminates its portion of the cycle with the formation of spores. It is *diploid*,<sup>2</sup> its cells having the double ( $2n$ ) number of chromosomes.

The complete cycle may be represented as follows :



The spores of the algæ exist immersed in water and may be free-swimming as in *Chlamydomonas* and *Ulothrix* (Fig. 55 C and D, p. 113) or non-motile as in *Dictyota* (Fig. 78, p. 151) and *Poly-siphonia*. In the land plants the spores are resistant to desiccation and are distributed by air. The gametes, on the other hand, remain restricted to water, which alone provides the necessary medium for the free-swimming sperms to reach the eggs. Only in the flowering plants has this necessity been overcome.

In the lowest group of land plants, the liverworts and mosses, the vegetative plant body is the haploid gametophyte. The liberation of sperms and fertilisation can only take place when there is a film of water over the thallus. When the resulting zygote germinates, the diploid generation produced never becomes an independent plant but remains, a mere spore capsule, attached to the thallus by its stalk. The spores are only liberated from the capsule when the atmosphere is dry, and they then become air-borne. The two methods of reproduction are adapted to two utterly different media and sets of conditions—the gametes to the old medium of water and the spores to the new medium of air.

<sup>1</sup> Greek ἀπλός (haplous), onefold.

<sup>2</sup> Greek διπλός (diploous), twofold.

In the more highly adapted land plants the relations of the two generations are reversed. The sporophyte, with its better adaptation to subaerial conditions, becomes the dominant partner; it is, in fact, the plant as commonly observed. The gametophyte is relatively inconspicuous and exists more and more under the protection of the sporophyte. *Dryopteris* well illustrates a plant with two free-living generations consisting of a dominant sporophyte and an inconspicuous gametophyte.

#### DRYOPTERIS<sup>1</sup> FILIX-MAS<sup>2</sup>

##### *The Sporophyte*

The diploid spore-bearing plants of the male fern are familiar inhabitants of shady woods and hedgerows, especially on the moister western side of our islands; they are often planted in north-facing garden borders. They consist of a cluster of large leaves, usually called fronds. Each leaf has a long rather woody central stalk and rows of leaflets spread on opposite sides of it. Each leaflet is called a pinna,<sup>3</sup> and is further subdivided into pinnules giving the frond a distinctly feathery appearance.<sup>4</sup> The leaf stalks come off from a short, stout rhizome (underground stem), which lies obliquely in the surface of the soil and appears even stouter than it really is on account of the decaying leaf-bases that surround it (Fig. 79 b). The old leaves are not shed, like those of the flowering plants, but rot away while still attached to the rhizome. The rhizome itself also dies and rots away behind, growing onwards continually at the apex. The main root also disappears at an early stage and is replaced by numerous adventitious roots emerging from among the leaf bases.

The fern sporophyte is a vascular plant and has elaborately

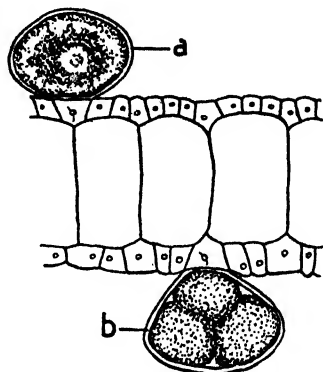


FIG. 78.—*Dictyota dichotoma*, tetraspores produced in sporangia on surface of the thallus. *a*, young sporangium; *b*, tetrad of four spores, one below the plane of section, in a mature sporangium.  $\times$  about 300. Somewhat diagrammatic.

<sup>1</sup> Greek δριος (drios), wood, thicket and πτερίς (pteris), a fern; the woodland fern—which it is. Also called *Aspidium* or *Nephrodium*.

<sup>2</sup> Latin, male fern; so called from its robust-looking fronds. *Athyrium filix-femina* is called the “lady fern” in comparison.

<sup>3</sup> Latin, a feather.

<sup>4</sup> The name fern is said to be derived from the Sanskrit, panna, feather,

specialised conducting tissues in which occurs transport of water to the leaves and of food materials away from them. About half a dozen vascular strands arranged in a circle just below the surface run down each leaf-stalk. In the rhizome the vascular strands take the form of a network (Fig. 80 B and C), each mesh corresponding with a leaf base. The bundles of the stalk enter and fuse with the strands of its corresponding mesh. Each strand contains two kinds

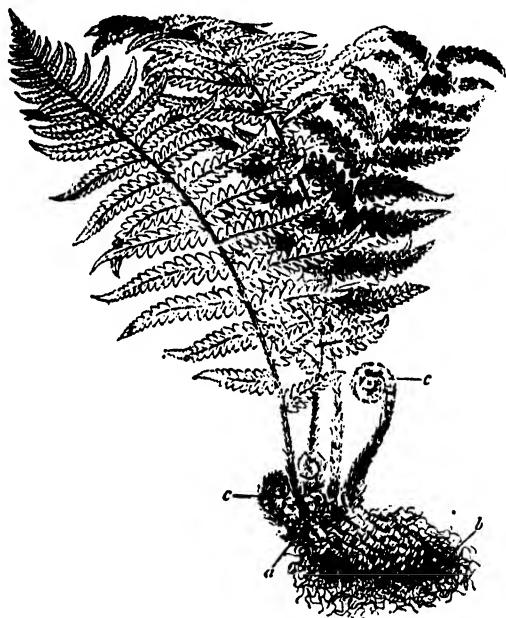


FIG. 79.—*Dryopteris filix-mas*, spore-bearing plant. *a* and *c*, young leaves in successive stages of uncoiling; *b*, stem more or less hidden in bases of old leaves and bearing numerous fibrous roots.  $\times 1/12$ . After Wilhelmj.

of tissue. The water-conducting tissue consists of xylem tracheids, long cells with "planed off" ends where they are attached to their neighbours. They have transverse bars of lignified thickening on their walls with thinner areas between, where only the primary cell membrane is present and through which passage of water readily occurs. The living contents are lost as soon as the structure of the walls is complete and water passes through the dead tubes remaining. Conduction of food materials goes on through sieve-tubes (Fig. 122) which become elongated but retain their living contents.

Towards its apex the rhizome is covered with the tightly-coiled stalks of young fronds (Fig. 79 *a* and *c*). The leaf stalk is formed

before the pinnæ, and is covered by an abundant coating of brown, chaffy hairs which remain on the mature stalk, but are not found on the pinnæ. The unrolling of the spiral as the stalk develops (Fig. 79 c) is a very unusual feature, characteristic of ferns.

### Spore Formation

Spores are produced on the under-surfaces of the fronds and in *Dryopteris* there are no other special differences of form between fronds that produce spores and those that do not; all are green and

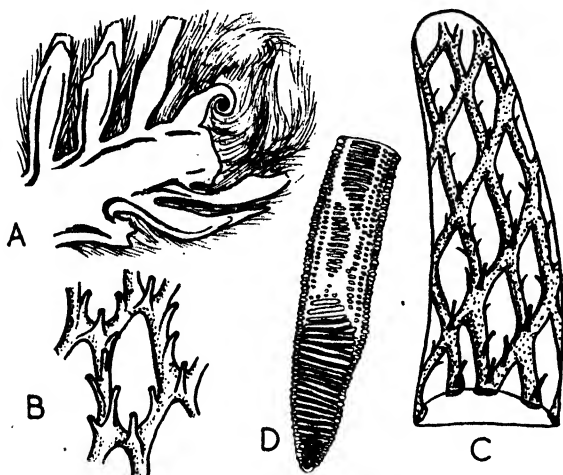


FIG. 80.—*Dryopteris filix-mas*. A, longitudinal section of stem apex with bases of young fronds and covering of numerous long hairs. B, one mesh of the vascular tissue seen more extensively in C. The smaller strands are the bundles entering from the leaf stalk. There is one leaf stalk to each mesh. D, one end of a typical fern tracheid.  $\times$  about 100. After de Bary. A, B and C after Sachs.

able to photosynthesise. In some fern species such as *Osmunda regalis*, the royal fern, fertile spore-bearing fronds are markedly differentiated from the vegetative fronds. The first-formed fronds of a young *Dryopteris* plant are always vegetative, but in a mature plant spores may be produced vigorously on all the leaves. They are developed in sporangia which are formed in clusters, called *sori*,<sup>1</sup> on the lower surface of the pinnules on each side of the midrib (Fig. 81A). Each cluster is covered by a kidney-shaped membrane outgrowth of the leaf surface, named the *indusium*.<sup>2</sup> Numerous spores are found in each sporangium. They are very minute and consist of a single cell with a nucleus, a colourless inner wall and a thick outer

<sup>1</sup> Greek *σῶρος* (*sōros*), a heap.

<sup>2</sup> Latin, a tunic.

wall, which becomes dark brown when ripe. They are formed in tetrads by meiosis and are therefore haploid (cf. table, p. 150).

Each sporangium is a biconvex capsule, with thin side walls consisting of a single layer of thin-walled cells. The greater part of the edge is occupied by the *annulus* whose cells have heavy thickenings on their inner and side walls, the outer walls remaining thin (Fig. 81 Bb). The rest of the edge of the sporangium, about one-third, is the *stomium* formed of large thin-walled cells (Fig. 81 Ba). In dry weather the ripe sporangia dehisce, casting out their spores by a

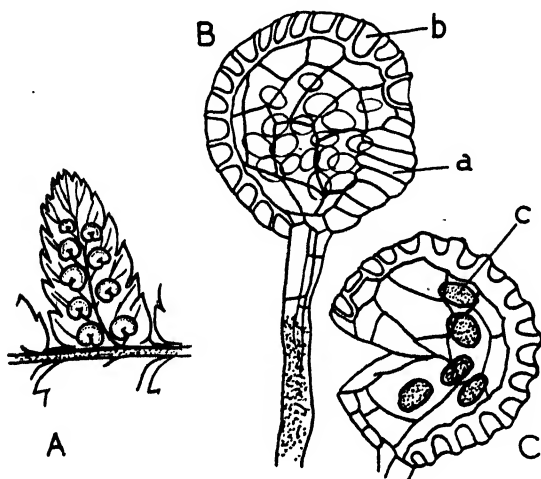


FIG. 81.—*Dryopteris filix-mas*. A, under-surface of a pinnule of a fertile frond with two rows of sori, each sorus covered by the kidney-shaped indusium seen in surface view.  $\times 2$ . B, a sporangium; a, stomium; b, annulus; spores are seen inside the transparent walls. C, a sporangium after dehiscence; c, spores not discharged.  $\times$  about 250.

mechanism of much interest. It depends upon the fact that water enclosed in a small space whose sides it permeates, exhibits great tensile strength. As water is lost from the annulus cells by evaporation through their thin outer walls, their volume contracts. The diminishing water does not come away from the walls but, owing to the strong molecular adhesions between water and cell-wall material, drags the thick side walls inwards towards each other especially at the free outer ends. The effect of this occurring all along the annulus is to cause it to straighten, tearing apart the cells of the stomium as it does so. This goes on until the tension in the water films becomes too great and they break. The annulus then snaps suddenly back into its original position, catapulting out many of the spores with the

jerk. The dry spores may be carried away on the wind and retain their capacity to germinate for long periods.

### Gametophyte

Spore germination occurs in moist and shady situations and probably only a minute percentage of air-borne spores fall on suitable spots. When they take up water and become turgid the outer coat is ruptured, and the colourless inner wall protruded. Rapid cell

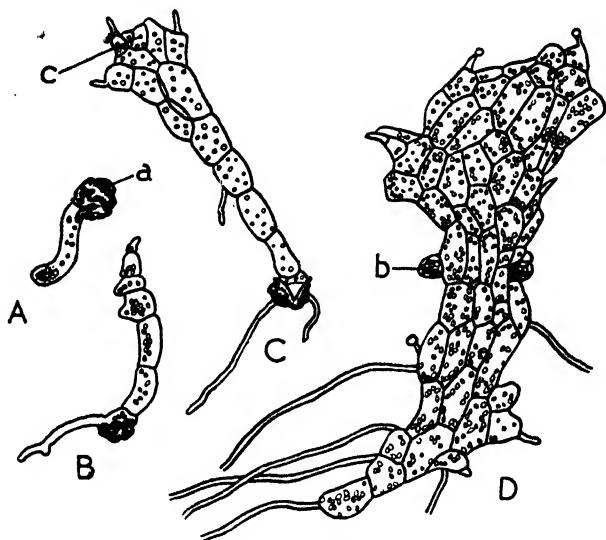


FIG. 82.—*Dryopteris filix-mas*, early stages in the development of the prothallus. A, protrusion of the inner wall of the spore; a, spore coat. B, formation of a filament of cells with chloroplasts and a colourless rhizoid. C, first divisions in the longitudinal plane; c, apical cell. D, young prothallus with rhizoids and b, antheridia.  $\times 250$ .

division follows which forms a short filament that soon develops into a flat plate with a single apical cell (Fig. 82). This becomes sunk in a notch, owing to the rapid division and enlargement of the cells on its flanks. The mature gametophyte, the *prothallus*, is heart-shaped as a result. On the two wings it is only one cell thick, but there is a cushion of tissue several cells thick at the centre. Hair-like rhizoids develop from the under-surface of this cushion, especially from its hinder end, and absorb moisture and mineral nutrients from the soil surface on which it lies. All the other prothallial cells are green, photosynthesising cells with numerous small chloroplasts, large central vacuoles and thin cell walls.

*Antheridia*

Sexual organs are formed on the lower surface of the prothallus. Usually both male *antheridia* and female *archegonia* are formed on the same individual but occasionally an attenuated filamentous prothallus is produced that develops antheridia only. In more normal prothalli antheridia are the first sexual organs to appear and, in a matured prothallus, they are to be found among the rhizoids in the older part of the central cushion. Each antheridium is formed from a single surface cell that enlarges and grows out from the general

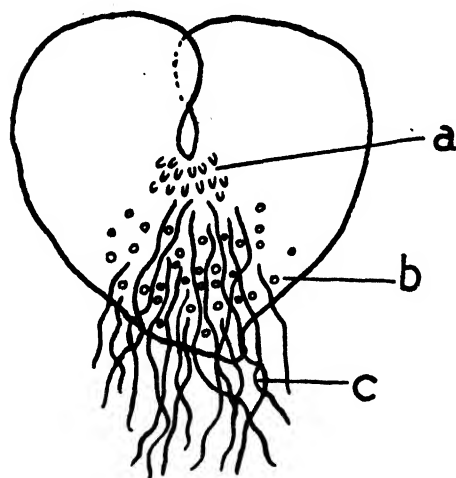


FIG. 83.—Diagram of underside of mature prothallus showing position of *a*, archegonia; *b*, antheridia and *c*, rhizoids.  $\times$  about 10.

surface. This cell divides to form a central cell surrounded by a wall one cell thick (Fig. 84). The central cell then divides to form a group of *sperm cells*, each of which contains a sperm inside a mucilaginous wall. The body of the sperm is formed from the nucleus of the cell, its very numerous flagella from the general protoplasm and, when the sperms escape, the mucilaginous wall is either sloughed off, or remains attached only to the hinder end of the escaping sperm. The

bursting of the antheridia with its consequent release of the sperms occurs only in contact with liquid water and takes place when a shower of rain gives rise to a film of water around and under the prothallus. The sperms swim freely in this moisture owing to the movements of their circlet of flagella.

*Archegonia*

The female organs are also formed by single cells of the lower surface that enlarge and divide. They appear rather later in the life of the prothallus than the antheridia and are therefore found nearer to the apical notch. The archegonia consist of neck and venter like those of *Pellia*, but the neck is shorter, being only four or five cells

long (Fig. 85). It hangs down towards the surface moisture of the soil and its centre is occupied by mucilage from a disintegrating row of cells. The venter contains a single egg in line with the mucilage

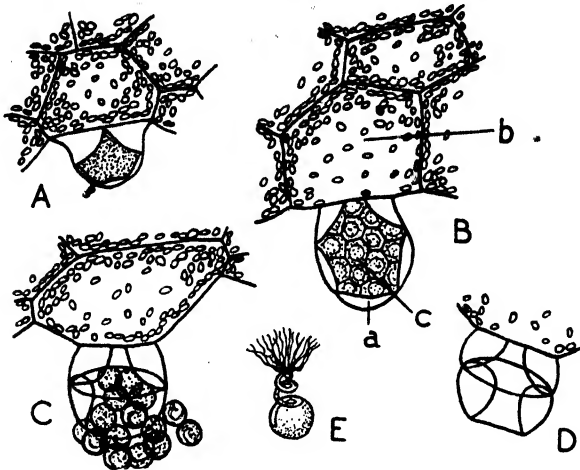


FIG. 84.—*Dryopteris filix-mas*, development of the antheridium. A, central cell and wall. B, after further divisions; *a*, cap cell; *b*, vegetative cell of prothallus; *c*, "sperm cells." C, sperm cells escaping after bursting off the cap cell. D, empty antheridium after dehiscence. All  $\times 400$ . E, free sperm. The last after Kny.

canal. The outer end of the neck bursts open in the presence of water; and sperms, escaping from antheridia and swimming in the surface film of moisture, are attracted, probably by the extrusion of malic

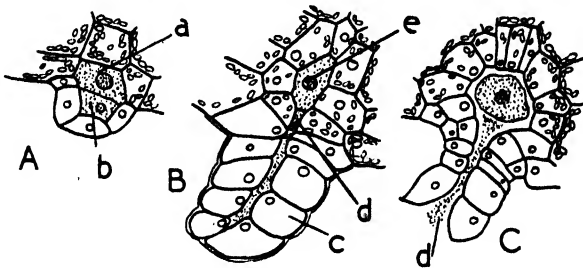


FIG. 85.—*Dryopteris filix-mas*, development of the archegonium. A, division of surface cell forming wall (unshaded); *a*, central cell and *b*, canal cell. B, later stage with *c*, completed wall surrounding disorganised cells of neck canal; *d*, ventral canal cell and *e*, egg cell in the venter. C, archegonium ready for fertilisation; *d*, extruding mucilage.  $\times$  about 180.

acid or other attractive substances. Fertilisation occurs when a sperm enters the neck of an archegonium and wriggles through the mucilage to the egg in the venter.



*Embryology*

The product of the fusion—the zygote—is not a resting stage, but divides at once like the zygote of *Fucus*. Repeated divisions follow until a comparatively massive embryo is formed. This remains organically in contact with the under-surface of the prothallus by means of an organ called the foot (Fig. 86 Ac). Stem and root apices soon become distinguishable and a rudimentary leaf (Fig. 86 Cg) of simple outline quite unlike the pinnate fronds of the adult fern plant. It is green and soon becomes capable of photosynthesis; the root enters the soil and so the young plant becomes self-supporting. The prothallus withers away as the young sporophyte grows larger and completes the cycle of two independent but unequal generations.

*Adaptation of the Fern to Land Life.*

It will be evident from the account just given of *Dryopteris* that its occupation of a relatively dry habitat is a sort of compromise. Though the sporophyte is well adapted to such positions, the inevitable gametophyte can only find the conditions it requires in shady places with surface moisture. The life history of a fern is thus an

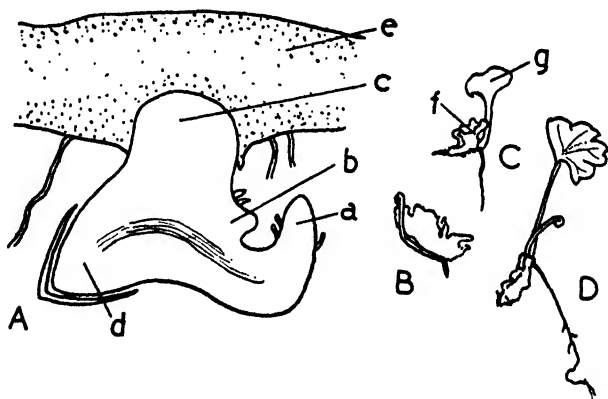


FIG. 86.—*Dryopteris filix-mas*. A, diagram of the embryonic sporophyte still attached to the parent prothallus; a, leaf rudiment; b, stem apex; c, foot; d, root apex; e, prothallus. After Hofmeister. B, C and D, stages of young sporophyte still attached to the prothallus; f, prothallus; g, first leaf of the sporophyte. In D, the first root is well developed, the second leaf appearing and the prothallus almost withered away.  $\times 2$ .

excellent example of an alternation of generations in which the two phases are adjusted to quite different conditions of life. It may be compared with the alternation of generations occurring in many

parasitic animals, in which the sexual phase and the asexual phase live in different hosts. In the fern, however, it must be remembered that the plant is still tied to habitats that are at least occasionally damp, because the sporophyte is dependent on the gametophyte during the early stages of its development, and must therefore start life in the same habitat. It is only by vegetative growth and propagation, as in the common bracken, that the sporophyte of the fern can spread into really dry places. If it is to reproduce sexually, the spores must return to damp conditions of life.

### Practical Work

(1) Examine a complete plant (**sporophyte**) of *Dryopteris*. Note the *leaves*, *stalk* and *pinnae*, and the numerous *adventitious roots* and examine the general shape of the short but bulky *stem*, more or less hidden by the *leaf bases*. Examine carefully an *unfolding leaf*. Make sketches.

(2) Carefully examine the under-surface of a leaflet bearing **sporangia**. Note the change of colour from the green *sori* near the tip to the brown ones that are fully developed. Sketch a single pinnule showing the *sori* with their covering *indusia* and the position of the *sori* on lateral veins.

(3) Examine and draw under the low power of the microscope a vertical section through a single **sorus** showing the attachment of the individual *sporangia* and the *indusium* with its "stalk."

(4) Examine individual **sporangia**. Many will dehisce while you watch if the section is a fresh one and is allowed to dry up.

(5) Examine and draw a single heart-shaped **prothallus**. Examine the lower surface under the low power of the microscope. Discover the *antheridia* among the *rhizoids* and the *archegonia* just behind the *growing point*. Mark the position of all these in your sketch.

(6) If prepared sections are available showing *antheridia* and *archegonia* make drawings of these marking the *wall cells*, and *sperm cells* of an antheridium and the *neck*, *mucilaginous strand*, *venter* and *egg* of an archegonium.

## Chapter XII

### HETEROSPORY THE LIFE HISTORY OF SELAGINELLA

#### *Pteridophyta*<sup>1</sup>

*Dryopteris*, described in the last chapter, is a good example of the ferns (*Filicales*), one of the principal groups of this great phylum of plants. Besides ferns it includes two other groups, the Club Mosses (*Lycopodiales*), and the Horsetails (*Equisitales*). These last two groups differ from the ferns in having small and simple leaves instead of large, compound fronds, which in the horsetails are so small that photosynthesis is mainly performed by the surface layers of the stem. Further, instead of bearing their sporangia upon the under-surface of the leaves like ferns, they have them associated with small leaves closely packed round the stems at the ends of shoots to form a cone or *strobilus*.<sup>2</sup> These special leaves of the cone are called sporophylls and differ in varying degrees from the normal foliage ones. The gametophytes of the club mosses and horsetails also differ very much in appearance from the flat prothalli of the ferns. Those of the club mosses are sometimes without any green colour and live saprophytically in humus or in humus-rich soils. These prothalli grow only very slowly and the sporophytes often achieve a large measure of independence of them by means of a vegetative propagation of their own parts. The common Field Horsetail (*Equisetum arvense*, Fig. 7) grows in hedge-banks and in neglected fields, usually in stiff, moisture-retaining clay soils. It is the only British member of the Pteridophyta to hold its own in such situations with the dominant seed plants. It does this so successfully as to become a pestiferous weed, difficult to eradicate. This it achieves not by means of rapid repetitions of its life-cycle, but by the growth of long underground stems, that spread widely and send up at intervals green aerial shoots, which become independent. Bracken (*Pteridium aquilinum*) is a fern which colonises sandy soils by similar means and with even greater success.

<sup>1</sup> See also p. 12.

<sup>2</sup> Latin, fir-cone.

The horsetails and many of the club mosses, *Lycopodium* for example, produce numerous spores all alike in size and behaviour and, in this, they resemble the ferns and the Bryophyta. A few of the club mosses, forming the genus *Selaginella*, have developed spores of two different kinds, that behave upon germination in two different ways. They are called *micro-* and *megaspores* in reference to their relative sizes. The development of heterospory<sup>1</sup> has had such important consequences in the plant kingdom that a clear understanding of

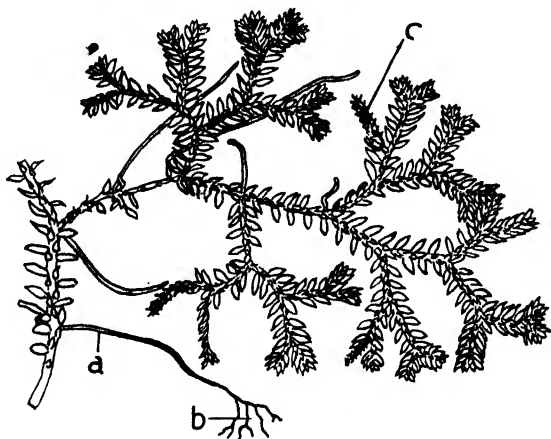


FIG. 87.—*Selaginella kraussiana*, showing creeping stem with leaves of two sizes. *a*, rhizophore; *b*, roots; *c*, cone. Nat. size.

it is essential. On no account must micro- and megaspores be confused with sperms and eggs. The essential difference is that *sperms and eggs fuse with one another* to carry on the life-cycle: *micro- and megaspores never fuse*. Sperms and eggs, being gametes, are haploid and both sorts of spores are diploid.

#### SELAGINELLA

*Selaginella* has many species which grow in humid tropical situations, but only one—*Selaginella selaginoides*—in Britain. It is found in moist mountain pastures of the north and west. Some of the tropical species are grown in greenhouses for the sake of their feathery appearance.

#### Habit

The following description is based on *Selaginella kraussiana*, a tropical species commonly grown in ferneries. It has a long stem

<sup>1</sup> Greek ἕτερος (heteros), other.

162. HETEROSPORY: THE LIFE HISTORY OF *SELAGINELLA*  
 which creeps over the soil and forms lateral branches at intervals. The roots do not spring directly from the stem but from a special, colourless organ, the rhizophore,<sup>1</sup> which comes off just behind each branching (Fig. 87 a). Each rhizophore has a bunch of adventitious roots at its tip. The leaves are small and are borne in unequal pairs. Each pair consists of a very small leaf coming from the upper surface of the stem and a somewhat larger one coming from below. In transverse section the leaves are seen to consist of upper and lower

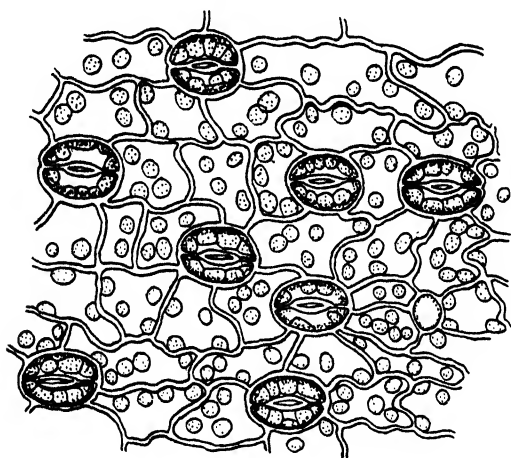


FIG. 88.—*Selaginella kraussiana*, upper epidermis of leaf over the midrib showing stomata.  $\times 330$ .

chlorophyll-bearing layers. The central tissue, *mesophyll*, consists of loosely packed cells each containing a single large cup-shaped chloroplast, with large intercellular spaces between. Pores, called *stomata*,<sup>2</sup> (Fig. 88), connect these spaces with the outside air. A conducting strand including elements of two different kinds runs along the midrib of the leaf. The *Selaginella* leaf thus includes specialisations associated with aeration and conduction which are not found in the simple leaves of the mosses and which are carried to much greater lengths in the flowering plants. They will be described more fully on page 223. The simple conducting strands of the leaf become more highly organised in *Selaginella* stems in ways that vary too much according to the species to be described here.

<sup>1</sup> Greek *ρίζα* (rhiza), root; and *φορέύς* (phoreus), bearer.

<sup>2</sup> Greek *στόμα* (stoma), mouth.

*The Cone*

The plant described above is the sporophyte and sooner or later it produces short, erect branches which end in cones (Fig. 87 c). These consist of special leaves, the *sporophylls*, closely arranged upon the stem. Each sporophyll bears a single, stalked sporangium at its base near its attachment to the stem. Beyond the sporangium is a small outgrowth called the ligule. The sporangia are of two different kinds,

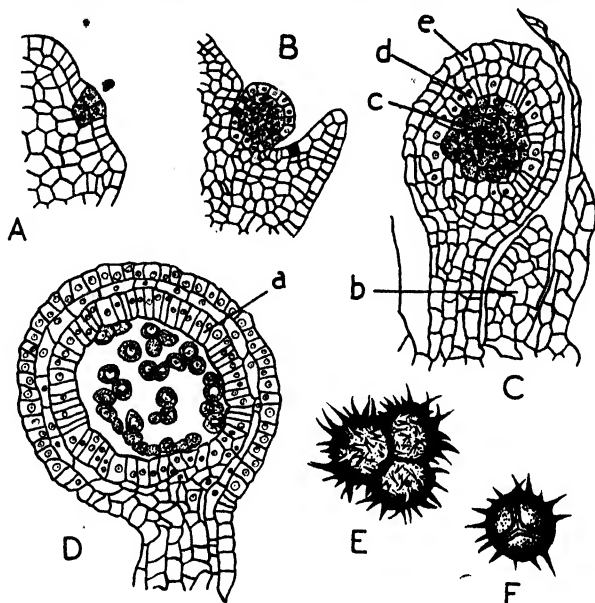


FIG. 89.—*Selaginella kraussiana*, development of the microsporangium. A, sporogenous cells shown with contents.  $\times 200$ . B, outer layer of jacket initials and archesporial cells inside.  $\times 200$ . C, later stage; *b*, the ligule; *c*, sporogenous tissue; *d*, tapetum; *e*, wall of two layers.  $\times 500$ . D, spore mother cells bathed in fluid secreted by tapetum *a*.  $\times 500$ . E, tetrad of microspores.  $\times 800$ . F, single microspore.  $\times 800$ . A and B after Smith. C–F after Stagg.

*microsporangia* and *megasporangia*, containing numerous small spores and four large spores respectively. Sporangia of both kinds occur in the same cone. The sporophylls are arranged in four vertical rows, two bearing microsporangia and two megasporangia. Different arrangements are found in other species.

*Microsporangia*

A microsporangium begins to form at the tip of a cone at the same time as its sporophyll. A group of sporogenous cells forms at the surface (Fig. 89 A), and by periclinal division gives rise to an outer

## 164. HETEROSPORY: THE LIFE HISTORY OF *SELAGINELLA*

layer of jacket initials and an inner group of archesporial cells. The outer layer becomes thick walled and cuts off a second jacket layer inside. The outermost archesporial cells cut off a layer called the *tapetum*<sup>1</sup> which does not develop into spores but forms a nutrient tissue (Fig. 89 Da). The remaining cells become spore mother cells and, except for a small proportion which may degenerate, form tetrads of microspores (Fig. 89 E).

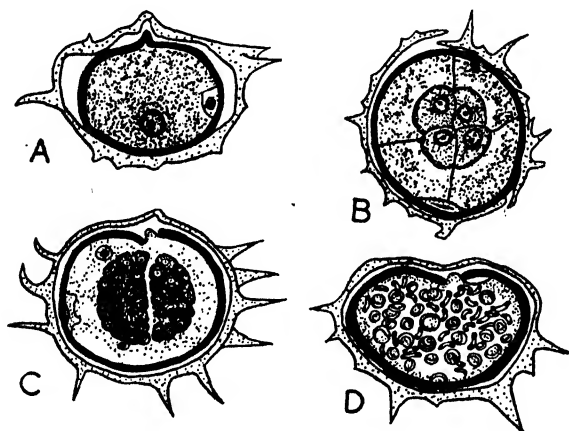


FIG. 90.—Development of male gametophyte and sperms. A, microspore with small prothallial cell on the right and antheridial initial in the centre. B, prothallial cell degenerating at the bottom and 4 of the 8 sterile jacket cells surrounding the 4 central (sperm-forming) cells. C, degeneration of the jacket cells and formation of sperm mother cells. D, sperms inside the microspore wall. After Stagg.

### *Male Gametophyte*

The microspores of *Selaginella* germinate while they are still enclosed within the microsporangium and their development into male gametophytes goes on *inside the wall of the microspore itself*. It is naturally very much restricted, the purely vegetative part of the gametophyte is represented by a single prothallial cell which is small and lens-shaped and is cut off by the first division of the microspore (Fig. 90 A). The larger daughter cell is the antheridium initial. It performs a number of divisions inside the microspore wall to form an outer layer of sterile jacket cells and an inner group of four cells that will divide further to form the sperms (Fig. 90 B). At this thirteen celled stage, the gametophyte, still enclosed in the microspore wall, is shed from the microsporangium. As a result of further divisions,

<sup>1</sup> Latin, a wall covering.

numerous biflagellate sperms are formed (Fig. 90 D), the jacket cells degenerate and the sperms swim freely inside the microspore wall.

### *Megasporangia and Female Gametophytes*

Megasporangia develop similarly to microsporangia until spore mother cells are formed. At this stage a difference sets in because most—and usually all but one—of the spore mother cells degenerate. The surviving cell gives rise to a tetrad of four large megaspores by meiosis. These germinate to form female gametophytes, starting while the spore is still enclosed in the megasporangium. The megaspore begins by enlarging and secreting a two-layered wall. The nucleus divides repeatedly, without wall formation, so that a multi-nucleate protoplast is formed lining the cell wall and surrounding a large central vacuole. Later, walls are formed starting at the top, and continued growth fills the central vacuole with cells. This is the female gametophyte or prothallus. While it is being formed the megaspore may be shed from the megasporangium: a portion of the spore wall cracks open and reveals the prothallial tissue inside. Where it is exposed it becomes green; but the gametophyte is already well stored with starch derived from the parent plant. Some of the exposed surface cells develop into archegonia and others into rhizoids (Fig. 91). The archegonia are of simpler construction than those of *Pellia* and *Dryopteris*, the neck being only two cells deep, and the venter is embedded in the prothallial tissue without a special wall of its own (Fig. 92).

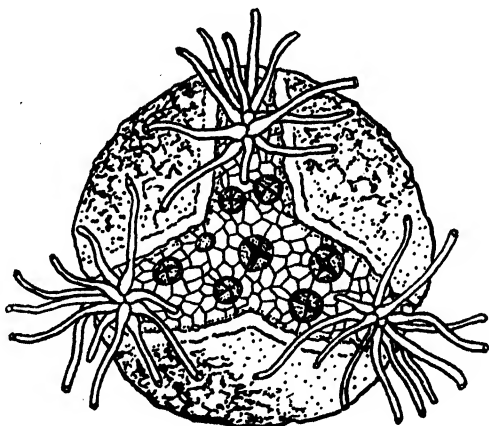


FIG. 91.—*Selaginella martensii*, female gametophyte inside the split wall of the megaspore. Surface view showing archegonia shaded and tufts of rhizoids.  $\times$  about 100. After Bruchmann.

### *Fertilisation*

Fertilisation occurs with the ripe female gametophyte, still enclosed in the megaspore wall, lying on the ground or lodged in the



megasporangium. Ripe microspores fall out of their sporangia and may lodge in open megasporangia or may drop to the soil. In wet weather the microspore wall breaks open and the free-swimming sperms inside escape. If there is sufficient moisture on the damp surfaces where they are lodged, they may be able to swim to the female gametophytes and their archegonia. Fertilisation occurs when a sperm enters the mucilage of an archegonium and wriggles down to the egg at the bottom. The resulting zygote germinates at

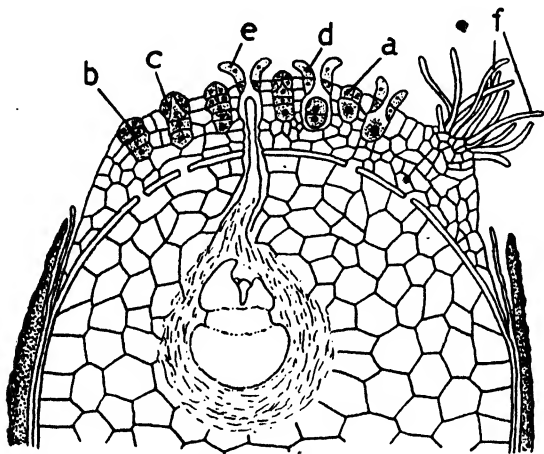


FIG. 92.—*Selaginella kraussiana*, vertical section of gametophyte protruding from split wall of the megaspore (shaded). *a*–*c*, archegonia in successive stages of development; *d*, showing first division of the egg; *e*, embryo pushed further down into prothallial tissue; *f*, rhizoids.  $\times$  about 160. After Bruchmann.

once and forms an embryo, which is pushed down into the prothallial tissue and nourished by it (Fig. 92 *e*) until it becomes self-supporting (Fig. 93).

The far-reaching reduction of the female prothallus involves the dependence of the young sporophyte embryo not only on the gametophyte, but even on the megaspore that produced it. Sometimes there is even a casual retention of the megaspore within the open megasporangium. There is, in other words, a more or less direct dependence of the sporophyte embryo upon the sporophyte generation that preceded it, owing to the reduction and retention of the gametophyte generation within a part of its parent. Pushed to an extreme, this would make the plant independent of free water for its fertilisation. *Selaginella* has not achieved this, although the microspores may roll about and mix with megaspores from other cones;

still, the final stages of fertilisation can only be achieved by sperms swimming through a water layer to the archegonia. Complete independence of this necessity could only result from retention of the megaspore in a megasporangium attached to the plant and by bringing the microspores to them. Only in such a position could the

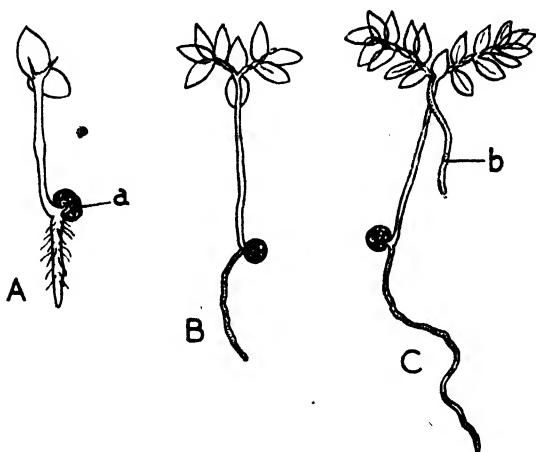


FIG. 93.—*Selaginella martensii*, embryos. A, first leaves and root; a, megaspore coat. B, stem branching, leaves of two sizes. C, showing first rhizophore at b.  $\times 4$ .

megaspores germinate secure from drying up and fertilisation occur without the help of external water. This step has been reserved for the flowering plants and is one of the reasons why they have become the earth's dominant race of plants. *Selaginella*, with its heterospory and reduced gametophytes is still tied to an at least semi-aquatic habitat.

### Practical Work

(1) Examine and draw the habit of a plant of *Selaginella*, preferably *S. kraussiana*. Note the trailing stem, leaves of two sizes, rhizophores, roots and erect stems terminating in cones.

(2) Dissect a cone, noting the arrangement of micro- and megasporophylls. Remove and, with the help of a hand lens, draw a micro- and megasporophyll each with its attached sporangium.

(3) Tease out, mount and draw under the microscope, microspores and megaspores.

## Chapter XIII

### THE SEED PLANTS THE LIFE HISTORY OF PINUS

The seed plants are divided into two main groups, Gymnosperms and Angiosperms. Both produce seeds in place of simple sporangia and gametangia, but they differ in their way of carrying them. The *Gymnosperms* bear them externally on the surface of megasporophylls which are aggregated into cones rather in the manner of the sporophylls of *Selaginella*. The *Angiosperms*, on the other hand, bear their seeds in enclosed structures probably formed by the fusion, edge to edge, of the megasporophylls. Many other differences will also appear.

The Gymnosperms are all woody trees or shrubs, perennial and, with few exceptions, evergreen. They include all the softwood and needle-bearing trees, firs, spruces, junipers, cypresses, redwoods, cedars and yews, as well as the less familiar cycads. Deciduous gymnosperms are the larches, maidenhair tree (*Ginkgo biloba*) and the swamp cypress (*Taxodium distichum*). They all have highly specialised leaves, stems and roots and a complex internal anatomy characterised by the possession of a complete double conducting system. One of the most familiar and best studied of this group is *Pinus*.

#### THE LIFE HISTORY OF PINUS

The genus *Pinus* has 80–90 species which are important members of the great forest belt of the northern hemisphere. Some of them are also found high up tropical mountains. In Britain, *Pinus*<sup>1</sup> *sylvestris*<sup>2</sup> is the Scotch Pine and is well known and appreciated for its red-barked bare stem and high branches with their irregular crown of dark green needle-leaves. It is a conspicuous feature of barren, sandy and gravelly landscapes.

The familiar tree, often reaching a great height, is the sporophyte and corresponds in this respect with the dominant generation of

<sup>1</sup> Original Latin name.

<sup>2</sup> Latin, wild, as distinct from cultivated.

*Selaginella* and the ferns and with the dependent sporogonium of the mosses and liverworts. It produces spores of two different kinds, microspores and megaspores which are segregated in different cones consisting exclusively of microsporophylls and megasporophylls respectively. Both kinds of cone are borne on the same tree, though often on different branches.

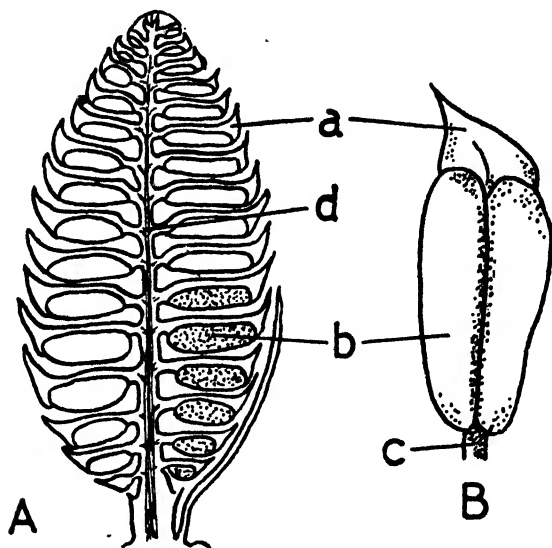


FIG. 94.—A, microsporangiate cone of *Pinus*.  $\times$  about 7. B, under-surface of a single microsporophyll.  $\times$  about 18; a, expanded and upturned tip of microsporophyll; b, microsporangia; c, stalk of microsporophyll; d, axis of cone. After Holman and Robbins.

### *Microsporangiate Cones*

The microsporangiate (sometimes called staminate) cones are borne as clusters of side shoots near the tips of young branches. They are yellow, about a centimetre long, and consist of an axis to which the microsporophylls are attached spirally. Each microsporophyll is formed of a stalk with an expanded distal end (Fig. 94) to the lower side of which two microsporangia are attached. When mature they are filled with numerous microspores.

The microsporangiate cones begin to develop near the tip of their branch. The microsporangia form in a fashion not unlike those of *Selaginella*. A primary wall layer is separated from the sporogenous tissue by periclinal divisions and, by further divisions, forms a wall several cell-layers thick and a tapetum. At the microspore-mother-

cell stage, the sporangium tissue becomes dormant and passes the winter without further divisions. Early in the spring meiosis takes place and the microspore (pollen) tetrads are formed. The microspores are thus complete in the season following the start of their development. They have a very characteristic winged shape owing to two lateral balloon-like outgrowths of the outer layer of their wall (Fig. 95 a).

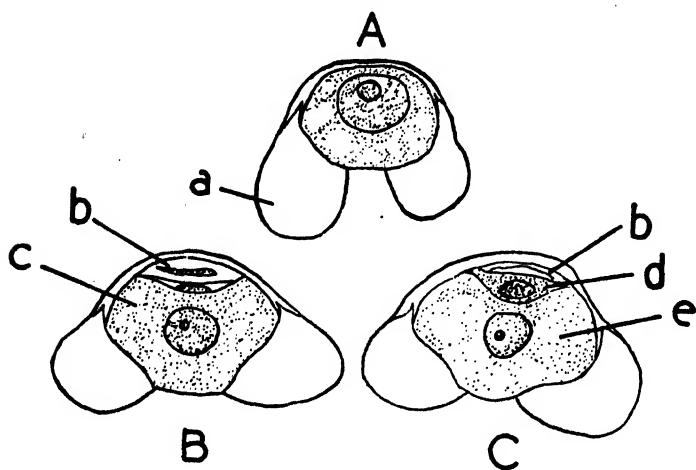


FIG. 95.—Pollen grains of *Pinus laricio*. A, mature grain with single nucleus; a, the wings. B, three celled stage; b, the vegetative cells; c, the antheridial cell. C, stage showing the degeneration of the vegetative cells; b, the remains of the vegetative cells; d, the generative cell; e, the tube cell. Somewhat diagrammatic. After Coulter and Chamberlain.

### Male Gametophyte

The microspores of *Pinus* germinate, like those of *Selaginella*, to give a male gametophyte and sperms which are retained inside the original microspore wall. At the time of germination the microspore proper has an oval section. Its nucleus divides into two; one daughter forms a small lenticular cell which becomes separated by a thin wall. It is pressed against the tough outer wall of the microspore and begins to disorganise. The other daughter nucleus enlarges and gives rise to a second lenticular cell which degenerates also. These two transient cells are all there is of the soma of the gametophyte. They are therefore called vegetative, or prothallial, cells (Fig. 95 b). The surviving cell is the antheridial cell and gives rise by a further division to the generative and tube cells (Fig. 95 d and e). In this condition there is a long pause until the following spring when the

microspores are shed from the opening microsporangia. The further events are described under the heading of pollination.

### *Megasporangiate Cones*

The megasporangiate (ovulate) cones, when they are ripe for fertilisation, are also about a centimetre long and are pinkish-brown.

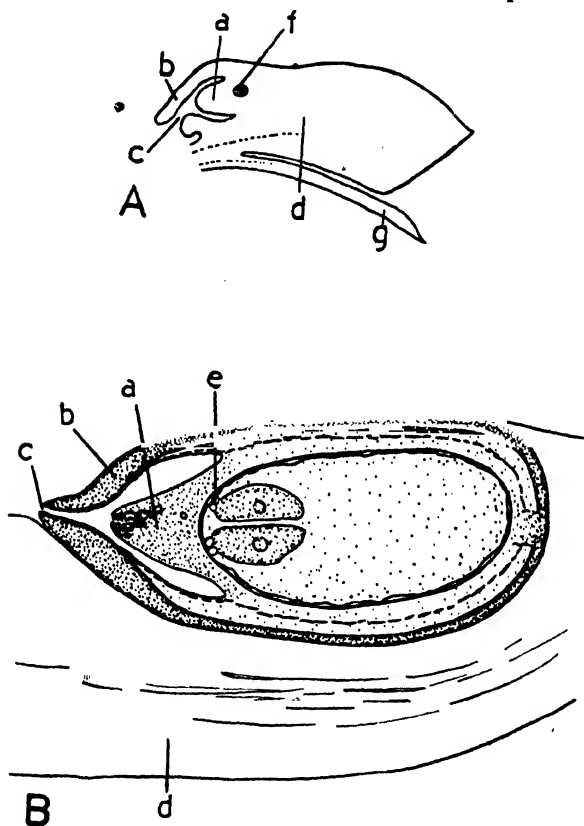


FIG. 96.—A, diagram of “megasporophyll” of *Pinus* in longitudinal section; axis of the cone towards the left. *a*, nucellus; *b*, integument; *c*, micropyle; *d*, ovuliferous scale; *f*, megaspore; *g*, bract. After Coulter and Chamberlain. B, similar section of the ovule at the time of fertilisation; *a*, nucellus showing tracks of pollen tubes; *b*, integument; *c*, micropyle; *d*, ovuliferous scale; *e*, archegonium.  $\times$  about 20.

They are found near the tips of branches and consist of megasporophylls arranged spirally round an axis. Megasporophyll may be a misnomer, since it is not certainly of leafy origin, but no alternative

name is better. Each consists of two parts, a scale above and a bract below (Fig. 96 A). On the upper side of the scale near its base are two small swellings, the *ovules*, which finally develop into seeds. A longitudinal section of a megasporophyll shows that the ovule consists of an egg-shaped block of tissue called the *nucellus* (Fig. 96 Ba) and an integument (Fig. 96 Bb) which overlaps the nucellus, leaving an opening, the *micropyle*, directed towards the axis of the cone. At the opposite end of the ovule, nucellus and integument are not distinct from the tissue of the scale.

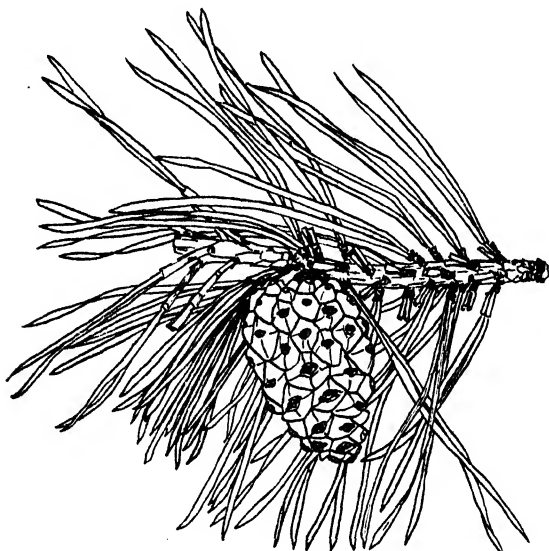


FIG. 97.—*Pinus sylvestris* shoot with a fertilised cone. The bracts are tightly sealed together and the cone has become pendulous.

At an early stage of development a single megaspore mother cell becomes conspicuous at the centre of the nucellus, which is therefore the megasporangium. The megaspore mother cell performs a meiosis to give a tetrad of megaspores each with the reduced number of chromosomes. The megaspore furthest from the micropyle enlarges and the other three degenerate.

### *Pollination*

In the spring of the third year of their development the microsporangia open by longitudinal splits and the pollen (microspores) is poured out. The amount produced by a large pine tree is enormous

and may amount to as much as a litre of fine yellow dusty powder. It is spread by the wind and may form a yellow coating over a wide area. Individual spores are believed to have been carried by the wind for hundreds of miles. Some small proportion of air-borne pollen is deposited upon megasporangiate cones and sifts down between the open megasporophylls to lie in close proximity to the micropyles of the ovules. A sticky fluid is secreted through the micropyle at this time from the nucellus. As it dries up the pollen grains are drawn in towards the nucellus and finally come into direct contact with it.

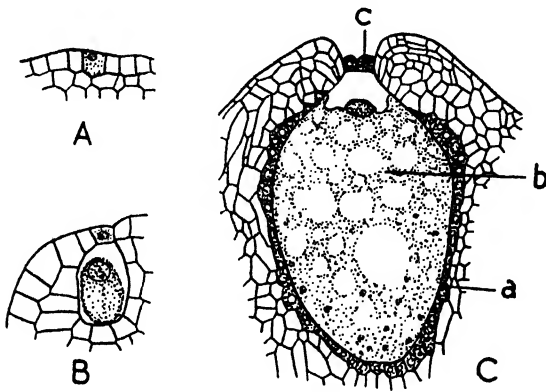


FIG. 98.—*Pinus laricio*, development of an archegonium. A, archegonium initial cell in the surface layer of the gametophyte tissue. B, neck cell and body cell formed by a horizontal division. C, body cell just before the ventral canal cell is cut off; a, tapetum; b, cytoplasm of the body cell with nucleus at top; c, neck cells. After Coulter and Chamberlain.

Soon after this happens, continued growth of the megasporophylls causes them to press against one another. They become tightly sealed together by a secretion of resin and the stalk of the cone curves so that instead of being upright it becomes pendulous (Fig. 97).

### *Female Gametophyte*

Inside the sealed-up cone the male gametophyte, resting upon the nucellus, slowly puts out a tube which penetrates into it. More active development goes on in the megaspore. It now enlarges at the expense of the surrounding nucellus and originates a number of free nuclear divisions following one after the other without wall formation, which sets in only after a considerable number of cells have been formed. The resulting tissue is the female gameto-



## 174. THE SEED PLANTS: THE LIFE HISTORY OF *PINUS*

phyte and now occupies a considerable space in the centre of the nucellus at whose expense it has grown (Fig. 96 B). About a year after pollination, archegonia—usually two in number—form at the end of the gametophyte nearest to the micropyle (Fig. 96 Be). They consist of a very large body cell (Fig. 98) and a neck only one cell deep, but with several cells in surface view. The surrounding tissue of the gametophyte grows up, so that the neck is embedded in a slight depression. A tapetal layer develops round the body cell (Fig. 98 Ca).

### Fertilisation

When the tip of the pollen tube (Fig. 99) at last reaches the archegonium the generative cell has divided into a stalk cell and two

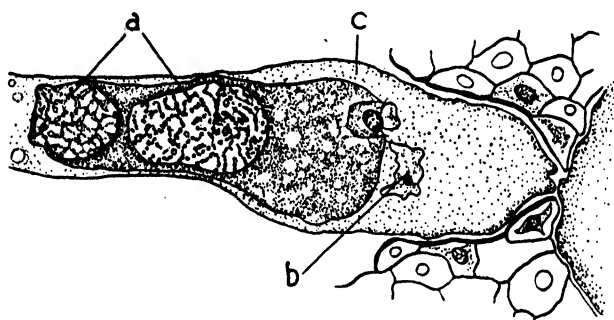


FIG. 99.—*Pinus strobus*, tip of pollen tube pushing between the neck cells of an archegonium. *a*, sperm nuclei; *b*, tube nucleus; *c*, stalk cell.  $\times 360$ . After Ferguson.

sperms; the tube therefore contains four cells, the *stalk* and *tube* cells and the two sperms (Fig. 99 a). The sperms are large nuclei with a little cytoplasm attached but no flagella. They are formed from the body cell only a few days before actual fertilisation occurs and at about the same time the body cell of the archegonium divides to form a small ventral canal cell, which at once disorganises, and a large egg cell with a conspicuous nucleus. Sperms and eggs are now ready for union; the tip of the pollen tube destroys the neck cells (Fig. 99), and all the four cells it contains are poured into the archegonium. One of the sperms comes into contact with the egg nucleus (Fig. 100 A) and fuses with it. Both nuclei begin a mitosis at the same time (Fig. 100 C–F) so that their two groups of chromosomes, twelve in each, become visible. By the time metaphase is complete all twenty-four are arranged upon a single equatorial plate (Fig. 100 E) and twenty-four daughter chromosomes pass to each daughter

nucleus—the diploid generation has begun (Fig. 100 H). So rapidly does this first division follow upon contact of egg and sperm that a zygote can scarcely be said to exist; growth to form an embryo, i.e. an infant plant with formed parts, follows at once.

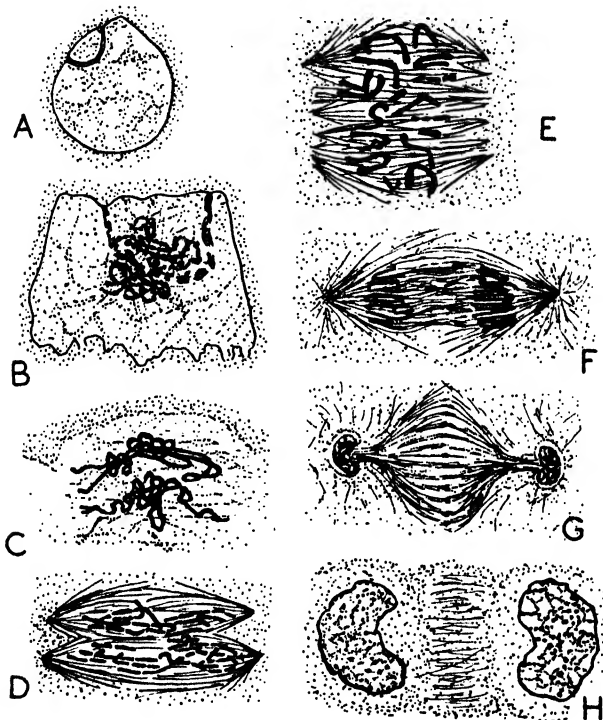


FIG. 100.—*Pinus strobus*, fertilisation. A, sperm nucleus, top left, fusing with egg nucleus. B, boundary between sperm and egg nuclei disappearing, chromosomes appearing in coils. C, beginning of mitosis in the still separate nuclei. D, two spindles formed. E, two spindles blending and chromosomes mixing at metaphase. F, anaphase on single spindle. G, daughter nuclei forming. H, daughter nuclei complete. A  $\times 100$ , the rest  $\times 360$ . All after Ferguson.

### The Seed

As the embryo grows, the ovule, and indeed the entire cone containing numerous fertilised ovules, grows to many times its original size. Details of the development are still largely lacking, but by the time the seed is ripe it has the structure shown in Fig. 210. Although more than one embryo may begin to form within an ovule, owing to its having several archegonia, usually only one completes the story.

It lies embedded in the much swollen gametophyte, now sometimes called the endosperm. A thin, papery layer surrounding it, the perisperm, is all that remains of the nucellus, and the integument has hardened into the testa. Finally the cone scales dry up and become



FIG. 101.—*Pinus canariensis*, seedlings showing numerous cotyledons. Seed coat still adhering at the right. About nat. size. After Dallimore and Jackson.

woody, and in doing so separate from one another so that the ripe seeds may fall out. When the seed drops out of the cone it usually has a thin membranous wing attached to it which splits off from the surface of the scale. This wing causes the seed to spin and so retards its fall and assists dispersal in a wind. Seeds falling on damp ground germinate and may eventually grow into the familiar trees. The seedlings have an unusual appearance on account of their many cotyledons (seed leaves), which make a striking contrast to the more familiar one or two of the flowering plants (Fig. 101).

The gymnosperms must be reckoned a highly successful group of plants. The number of their species, about 500, pales into insignificance beside the 150,000 or so of the angiosperms; but as individuals they abound and are the dominant plants over vast areas of the world's forests. This they owe, no doubt, to many factors that we can only follow in a very limited degree. Among them must be their massive growth enabling them to compete successfully with other plants for light and air and standing-room; and the elaborate organisation of their tissues, which in turn makes possible so great a living structure. On the reproductive side, their possession of the seed habit has made them free of a much wider range of habitats than even the ferns. Not only has the pollen tube done away with the need of a free watery medium in which

flagellated sperms may swim, but the retention of the female gametophyte within the body of the dominant sporophyte has withdrawn the delicate gametes from the danger of desiccation. Further, it is not only the gametophyte which is thus protected, but also the early stages of the new sporophyte, the embryo, which is protected and nourished at the expense of the parent sporophyte until the stage of temporary dormancy and shedding of the seed is reached.

These are factors clearly of great importance in giving the plant races possessing them the freedom of the earth's surface. They are shared and indeed possessed in an even higher degree by the flowering plants (angiosperms) to be described in the succeeding chapters. Significant as they are, we must not be misled into thinking them a whole answer to the problem of success and failure in the world of plants. Races with massive stems, the ancestors of the horsetails; and races with seeds, such as the Pteridosperms, have vanished utterly from the face of the earth. The maidenhair tree, with both advantages, is the last survivor of its race and has been kept in existence only by the piety of Chinese priests and the interest of horticulturalists.

It might be supposed that the long story of the emergence of plants from the water to the land is now old history and of little importance to the botanist studying the plants of to-day. A moment's reflection will show how far this is from the truth. Except in the light thus gained, the cones of the gymnosperms and, more important, all flowers are insoluble mysteries; cell structure and cellular relations with the outside world become more difficult to understand. Even for the most highly organised of land plants, their relations with water remain one of the dominant factors in determining their activities and distributions.

### Practical Work

(1) Examine a **spring shoot** of *Pinus sylvestris*. Note the *needle leaves* borne on short shoots or *spurs*; and the *microsporangiate cones* borne instead of spurs towards the base of the current year's growth. On a similar shoot note the young *megasporangiate cones* borne erect as branches near the tip of the new growth. On the second-year growth note the larger *fertilised cones* that have become green and pendulous. Examine also *mature cones* that have become brown and woody and whose scales have opened exposing the *winged seeds*.

(2) Dissect out a *microsporangiate cone*. Make drawings showing the *axis* with a few *microsporophylls* still attached. Make a drawing of a microsporophyll from below, showing the *stalk*, *expanded end* and two *microsporangia*.

(3) Tease out some *microspores* and examine under the microscope. Note their characteristic form with lateral wings.

(4) Dissect out a young *megasporangiate cone*. Draw a *bract* from above showing the two ovules at its adaxial end.

(5) Examine a **prepared** longitudinal section of an *ovule* ripe for fertilisation. Make a labelled diagram showing the *micropyle*, *integument*, *nucellus*, *female gametophyte* (endosperm) and *archegonia*.

(6) Pull **ripe seeds** out of an opened woody cone. Make a drawing showing the seed and the *membranous wing* attached to it that splits off from the surface of the cone scale.

(7) Examine and draw Pine (or Yew) **seedlings** showing the numerous cotyledons.

## Chapter XIV

# THE FORMS AND LIFE HISTORIES OF THE FLOWERING PLANTS

The existing species of angiosperms or flowering plants are very numerous—there are about 150,000 of them—and they are exceedingly various in their forms and in the details of their life histories. They have spread over almost the whole of the world's land surface. Only the extreme polar zones and waterless deserts, a few mountain tops and vertical cliffs have defeated them. This wide ranging has been associated with the development of a correspondingly great variety of life histories and forms.

### *Monocarpic and Polycarpic Plants*

The typical flowering plant, just like any of the lower types, first germinates, then has a period of active vegetative growth and after that a phase of reproduction, i.e. flowering. This may terminate the life of the individual but, since it possesses a highly developed soma does not necessarily do so. The plant body may survive the crisis of reproduction and go on to a further period of vegetative growth, followed by further reproduction and so on. The existence of *polycarpic*<sup>1</sup> plants of this latter kind is potentially indefinite and, in the actual example of forest trees, may cover thousands of years and the production of an enormous bulk. Plants which flower once and then die are said to be *monocarpic*<sup>2</sup> and include most of the short-lived, non-woody species. They usually accumulate a reserve of food materials during their growth period which is exhausted during flowering and fruit formation.

Many monocarpic plants, living in temperate zones with a well-marked rhythm of seasons, pass through their cycle in a single growing season and die down, so that the species is carried through the winter only by its seeds. These are the *annuals*, which form so large

<sup>1</sup> Greek πολὺς (polus), many; καρπός (karpos), fruit.

<sup>2</sup> Greek μόνος (monos), single.

a part of ephemeral quick-growing florals and of the summer show in gardens. The monocarpic plants of the greatest importance to the human race are the cereals.

Some monocarpic plants delay flowering beyond the limits of a single season, survive the winter in a dormant state and flower after a second period of growth. These are the *biennials*. Many biennials like beets, carrots and turnips are important food plants. They are used at the end of their first season of growth for the sake of the food reserves which they possess at this stage laid up in special storage tissues.

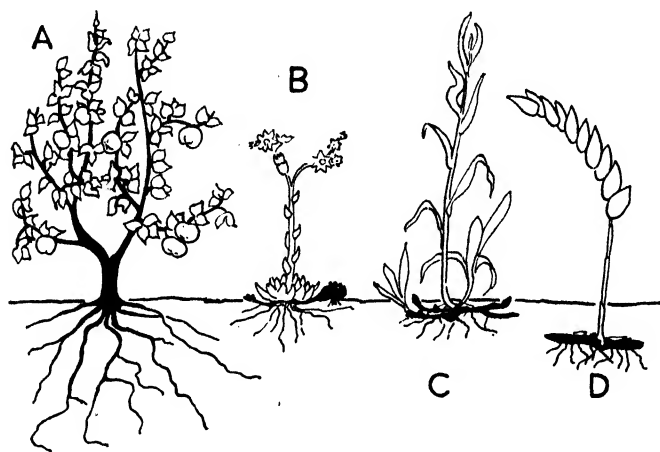


FIG. 102.—Life forms of flowering plants. A, exposed plant with deciduous leaves. B, surface plant, cushion type. C, half-hidden plant. D, hidden plant, rhizome type. Diagrams based on apple tree, *Sempervivum*, michaelmas daisy and Solomon's seal respectively. Varying scales. Persistent parts shown black.

Most polycarpic plants and a few monocarpic—like the so-called century plant—are perennial, i.e. they survive from one growing season to the next over a varying number of years. Some are short-lived and some very long-lived. Various methods of surviving the unfavourable winter season are common; four main types with increasing degrees of protection are as follows:

(a) *Exposed plants*, such as trees and shrubs have tough resistant outer coverings especially developed over the resting buds and other young tissues destined to carry on the growth of the plant. They may be deciduous, i.e. shed their leaves during the unfavourable season, or, failing that, have leaves of special construction (Fig. 102 A).

(b) *Surface plants* have their perennating buds close to the ground where they are less exposed than those of the previous group and may be protected by snow or litter. Tall growing parts, if any, are cut back to varying degrees according to the severity of the winter. Plants of this group vary from roses, whose flowering shoots die back at the end of the season and are replaced by new ones shooting from low down on the old stems, to the cushion plants typical of alpine regions and beloved of rock gardeners (Fig. 102 B).

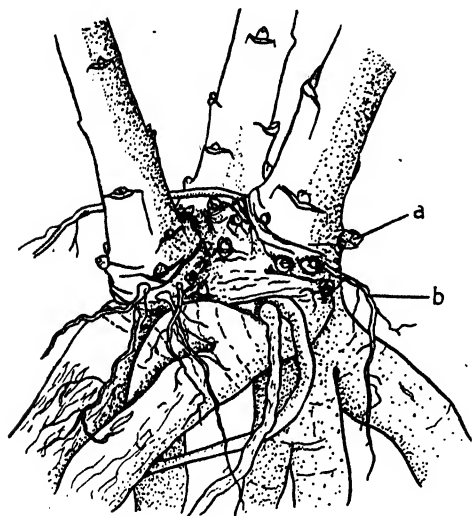


FIG. 103.—Rootstock of *Atropa belladonna*, bearing three large aerial shoots of the current season. *a*, adventitious buds from which similar shoots will be formed in the following season; *b*, adventitious roots.  $\times$  about  $\frac{1}{2}$ .

(c) *Half-hidden plants* achieve a greater degree of protection than either of the two previous types by having their perennating buds actually in the soil surface where they are protected by the surrounding soil, litter and withered remains of the aerial parts of the plant itself. Many garden perennials like sunflowers and michaelmas daisies are of this kind and it is indeed the dominant group in countries such as our own where winters are semi-severe and extreme drought is infrequent (Fig. 102 C). Rosette

plants, whose whole vegetative body is closely appressed to the soil, afford many successful members of this class.

(d) *Hidden plants* pass the winter wholly underground or, if swamp plants, under water. They are the most fully protected of all these groups of plants and the underground types are found in regions where there are prolonged seasons of drought as well as of cold. The characteristic modification of this group is the *rhizome*, i.e. the shoot which grows horizontally underground, usually at a more or less fixed depth below the soil surface (Fig. 102 D). The leaves of this shoot are modified or rudimentary and obviously unable to photosynthesise. It is nourished by aerial shoots which are

joined to it and which die away in the unfavourable season. The next season's shoot, and often the flower as well, spring from the rhizome utilising reserves of plastic materials that have been accumulated. Food storage on this extensive scale is associated with special modifications of the rhizome into tubers, corms or bulbs. It may also occur in a *rootstock*, i.e. a large swollen root usually capped by a condensed stem from which new leaves and branch shoots are produced annually. Typical examples are dandelions, monkshood and belladonna (Fig. 103). The swollen "roots", of carrots, parsnips and other culinary plants are similar, but survive only a single winter.

#### THE ERECT HERBACEOUS ANNUAL

This is the simplest type of flowering plant. It grows rapidly during the favourable season and passes through the unfavourable as a dormant seed. Its vegetative body, therefore, has no special modifications or adaptations for passing the winter.

The body of a simple annual consists below ground of a descending tap-root (Fig. 104 *tr*) and its branches or side roots of successive orders. These penetrate the soil, fix the plant in position and

absorb salts and water from the soil solution. Above ground there is the shoot, consisting of a vertical stem carrying foliage leaves at the nodes, and side shoots, or branches originating in the axils of the

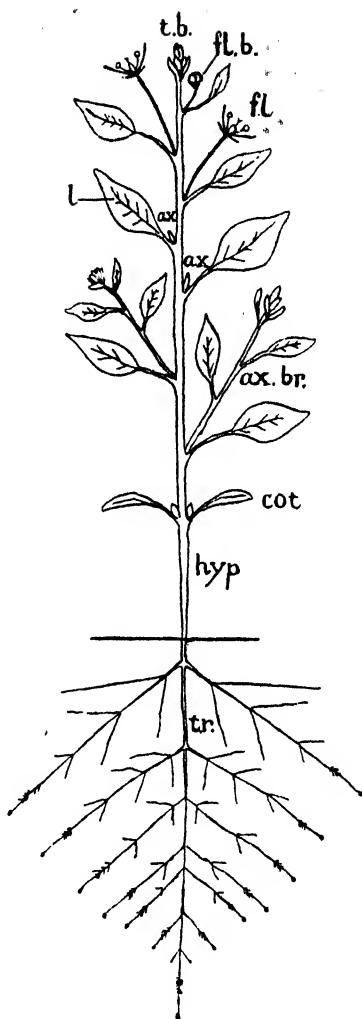


FIG. 104.—Diagram of an erect, herbaceous annual. *ax*, axillary bud; *ax.br.*, axillary or lateral branch; *cot*, cotyledon; *fl.*, flower; *fl.b.*, flower bud; *hyp*, hypocotyl; *t.b.*, terminal bud; *tr.*, tap root.



leaves. The roots and stems are typically cylindrical though the latter may be angled or flattened, and the leaves are typically flat laminæ whose variation of shape according to species is all but limitless.

The first leaves borne by the stem—those nearest to the root—are paired or single according to whether the plant belongs to the great group of the dicotyledons or to the monocotyledons. They (or it) are already formed in the embryo present in the dormant seed. The axis below these cotyledons and above the root is the hypocotyl (Fig. 104 hyp) and differs from both root and stem in its structure. The stem is terminated by the terminal (or apical) bud where growth is going on. Dormant axillary buds are usually to be found in the leaf axils, if they have not already grown out into lateral shoots.

Eventually flowers are produced. These are special shoots bearing specialised leaves—the floral leaves—frequently much modified in appearance from the foliage leaf. Some of them, the stamens and carpels, behave as sporophylls; some, the petals, as conspicuous envelopes and others, the sepals, as protective ones. The entire flower begins as a flower bud which is distinguishable at an early stage from a foliage bud. After fertilisation has taken place the essential parts of the flower, principally the carpels, become modified to form the fruit. The outer whorls of sepals, petals and usually even the stamens wither and drop away. Inside the fruit, the ripe seed is produced and, if the plant is monocarpic, the life-cycle is complete and the plant itself dies.

#### PERENNIALS

Perennials of the exposed type may resemble erect annual forms with the addition that they pass through a further edition of the annual cycle each year they survive. Usually they become woody, and so develop into shrubs or trees. The complex processes involved are described in Chapter XX. The surface types are also rather similar, but the half-hidden and fully hidden plants develop a variety of special forms that need further description.

#### *Runners*

A runner is formed when an axillary bud near the ground gives rise to an axillary shoot that grows rapidly and more or less horizontally outwards (Fig. 105). It is usually not a rigid structure and soon its tip touches the ground and the bud there sends out adventitious roots which anchor it to the soil. A young plant, or *offset*, is

then organised which may send out further runners in its turn. The connecting stems eventually rot away and a row of independent young plants is established. Strawberry plants send out runners freely and are usually propagated by their means. A less desirable runner plant is the creeping buttercup (*Ranunculus repens*), which spreads rapidly and tenaciously over wet clay soils by its runners. Brambles arch more highly, but their stem tips root in the same way and a bramble thicket is soon built up from a single plant. The runner habit clearly contributes notably to the success of these plants.

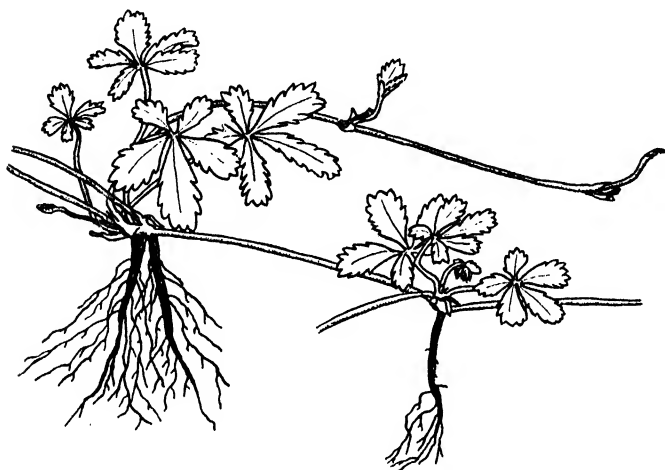


FIG. 105.—*Potentilla reptans*, runner developing adventitious roots at the nodes.  $\times 3/4$ .

### Rhizomes

Rhizomes are shoots growing below the surface of the ground and, in one form or another are the leading characteristic of the hidden and half-hidden plants capable of enduring extreme conditions of winter cold and drought, broken by short periods favourable for active vegetation. Rhizomes are most commonly produced by axillary buds of a young seedling growing out at first horizontally and then plunging below the surface of the ground (Fig. 106). When the rhizome reaches a particular depth below the surface its growth becomes horizontal again; and it tends to maintain this depth if the ground level is altered artificially, or, more naturally as in rapidly accumulating peat or sand dunes. The depth maintained varies in different species from the actual surface down to several inches. It is determined as a light-response of the branches or leaf stalks which

come above ground level. Each rhizome-forming species tends to keep a fixed length of its vertical members out of the light, which in normal circumstances means below ground. By covering the emerging shoots as they come up and keeping them in dark jackets the rhizome is caused to grow upwards in the soil.

The leaves of the rhizome are reduced to mere scales (Fig. 107 Aa) and have no green colour unless they emerge above ground on long stalks like those of *Dryopteris* (Fig. 79, p. 152). The tip of the rhizome may go on growing more or less horizontally underground year after year, sending up side shoots at intervals (Fig. 107 A). These

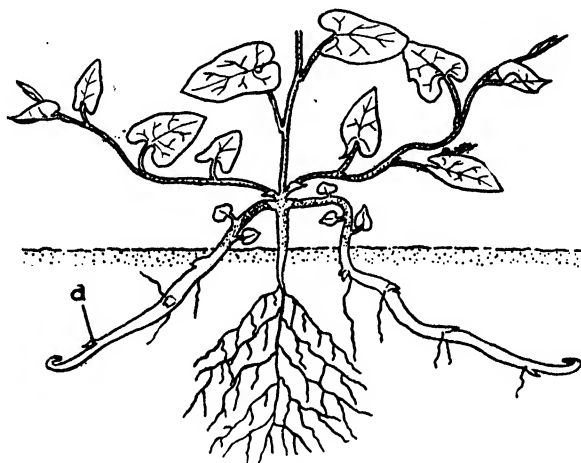


FIG. 106.—Young plant of *Convolvulus arvensis*. a, lateral shoot forming a rhizome.  $\times$  about  $\frac{1}{2}$ .

emerge above ground, and form normal foliage leaves which photosynthesise sugars, much of which passes into the rhizome. Eventually flowers are formed, and at the end of the growing season the aerial shoots die down and the plant lies dormant in the soil as the rhizome. Growth carried on like this year after year by the same apical bud is called monopodial; a twig of horse-chestnut, for example, is an aerial monopodium.<sup>1</sup> A slightly different cycle is followed by many rhizomes in which the apical bud itself turns upwards and produces a single aerial shoot. The subsequent growth of the rhizome is carried on by a lateral bud (Fig. 107 B). Since several buds co-operate successively in the growth of the rhizome itself, this type of growth is called sympodial. A familiar garden example is the iris.

<sup>1</sup> Latin, (a table) with one foot.

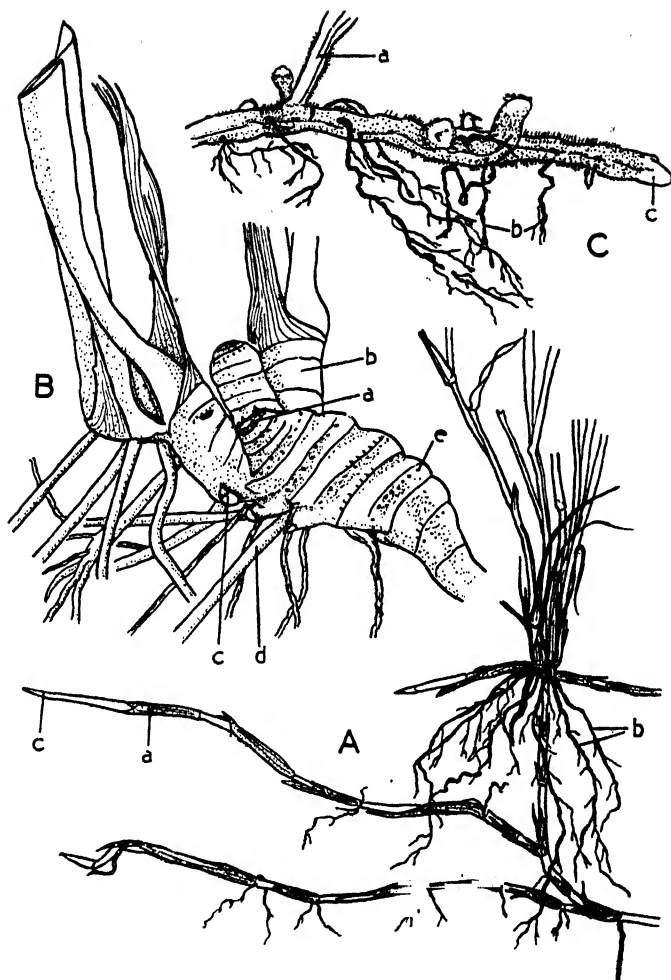


FIG. 107.—Rhizomes. A, *Agropyrum repens* (squitch), monopodial rhizome; a, scale leaf; b, adventitious root; c, apical bud. B, *Iris*, sympodial rhizome; a, apical scar; b, lateral shoots of the current year; c, lateral bud of the current year; d, adventitious root; e, wide leaf scar showing marks of vascular bundles. C, *Pteridium aquilinum* (bracken) rhizome; a, base of frond; b, adventitious roots; c, apex. All  $\times \frac{1}{2}$ .

Many troublesome weeds, i.e. plants so successful in growing that they are difficult to eradicate from positions where they are not desired, are rhizomatous. Bindweed (*Convolvulus arvensis*), squitch (*Agropyrum repens*), bracken (Fig. 107 C) and nettles are among the

major troubles of the farm and garden. They owe this to the fact that during dragging-out operations any small part broken off and left in the soil is usually able to propagate vegetatively and form a new plant. Such weeding, carelessly carried out, may be of actual assistance to the plant. The rhizome habit of the grass *Psamma arenaria*, and of the figwort (*Mesembryanthemum*) has been turned

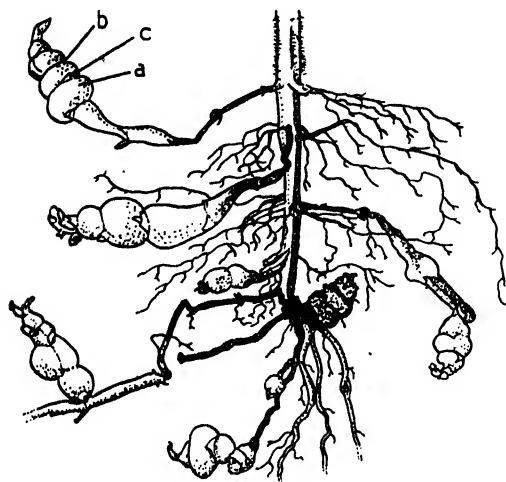


FIG. 108.—*Stachys tuberifera* tubers with swollen internodes, *a*, and constricted nodes, *b*, with triangular scale leaves, *c*.  $\times \frac{1}{2}$ .

to account in binding sand dunes and crumbling cliffs. The most delectable of the rhizome plants is *Asparagus*.

### Tubers

When the food reserves of the rhizome are localised in a particular part of it that becomes swollen by the development of abundant parenchyma, the swollen part is called a tuber.

Tubers may be separated by unswollen parts of the rhizome. The Chinese artichoke (*Stachys tuberifera*) develops a series of swellings which are the internodes of the rhizome, separated by constrictions at the nodes which do not swell (Fig. 108). The nodes can be readily recognised as such because they bear alternating pairs of triangular scale leaves. The internodes of the youngest part of the rhizome are not yet swollen and the terminal bud turns up to produce the next aerial shoot of the sympodium. The lateral buds, which continue the underground growth, grow out to form several thin internodes first, and then tuberisation of the internodes begins again. The tubers are thus connected together in branching chains.

Potatoes (Fig. 109) are the most familiar of all tubers and, humanly speaking, the most important. Their lateral shoots are formed from buds in the axils of basal leaves. They grow down into the soil and their tips begin to swell up and form tubers (Fig. 110). A moist atmosphere and absence of light tend to cause tuber forma-

tion from lateral buds; so that potatoes can be produced above ground by suitable enclosure of the lower region of the stem. A more usual and practical method of getting the same result is to draw up earth round the lower buds. Without such earthing-up a very poor potato crop would be obtained.

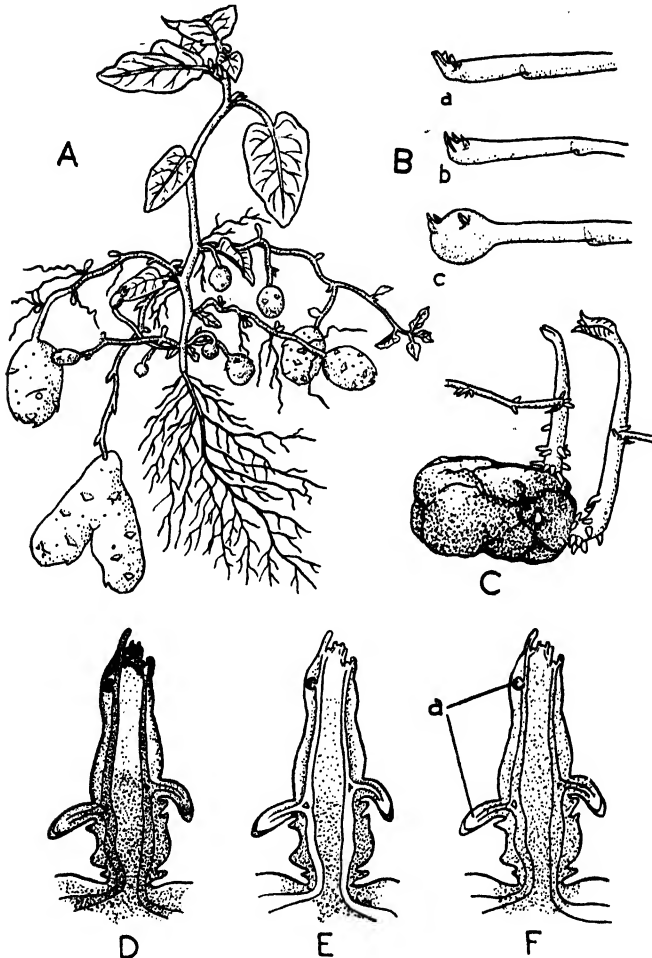


FIG. 109.—Potato. A, seedling plant forming tubers at the tips of lateral shoots. B, stages in the swelling of the shoot tip to form a young tuber. C, old tuber sprouting from the eyes. Two shoots with numerous adventitious roots have been formed, and a third bud is beginning to sprout. D–F, longitudinal section of a young shoot showing *a*, several young roots. The shading in D indicates the distribution of protein, in E starch and in F sugar. A and B after Troll. D–F after Penston.

When it is very young—about the size of a pea—the tuber bears minute scale leaves (Fig. 109 B); but these do not grow larger, though the body of the tuber swells, nodes and internodes alike. When the potato is full-grown, only the scars of the scales are visible with a depression (the axil of the leaf) above, containing several buds. These depressions are the so-called “eyes” of the potato. The

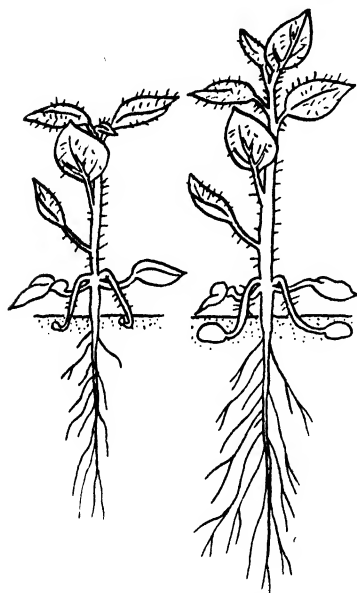


FIG. 110.—Young potato seedling showing origin of tubers on lateral shoots. After Nelson.

“rose” end of the potato, where the eyes are more closely crowded, is the apex. The eyes are inserted on a spiral which opens out as it is traced backwards into the region where more growth and swelling has had time to occur.

Potatoes left in the ground become isolated from the parent plant by the rotting away of the thin parts of the rhizome behind the tuber. In the following season they sprout from one or more of the eyes (Fig. 109 C). The young axillary sprouts throw out clusters of adventitious roots, into which nutritive substances pass from the body of the tuber (Fig. 109 D, E and F) and a new plant is thus established. This is the common means of propagation of *Solanum tuberosum*, reproduction by seed being rare and only practised artificially for breeding.

### Corms

A rather different type of stem swelling associated with the accumulation of food reserves is the corm. This is always situated at the base of an erect aerial shoot and usually involves several nodes and internodes. As the growing season progresses the base of the stem swells and becomes glutted with starch (Fig. 111 A). The leaves are chaffy brown scales that form an insulating layer over the swelling stem. At the end of the season the aerial shoot dies down, leaving an apical scar at the top of the corm. By degrees this becomes filled up and obliterated by the growth of a new axillary bud, which then spuriously acquires the appearance of being terminal. In this

condition the corm passes the winter or season of drought, and later renews the life of the plant by the sprouting of one or more of the axillary buds to form shoots similar to the original. At the same time a ring of roots appears from the base of the corm. The new shoots begin to swell and form new corms at their bases often before the old has been exhausted. The new corm lies above the old one, and so nearer the surface of the soil. It produces stout lateral roots that

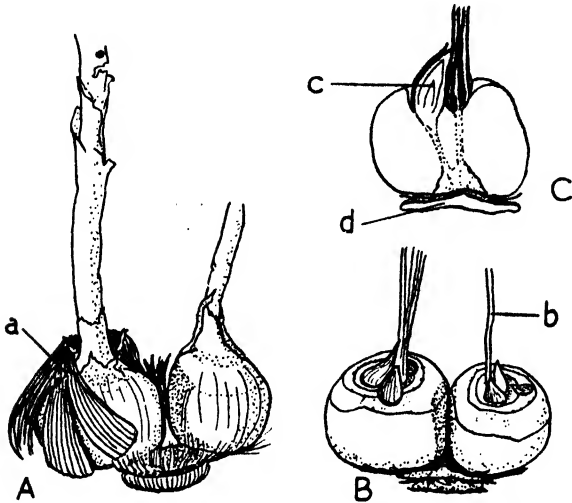


FIG. 111.—Crocus corms. A, two mature corms showing remains of previous season's corm at base; *a*, scale leaves peeling away. B, corms with scale leaves completely removed, the nodes showing as thin lines round the corm. Several buds formed in the axils of the scale leaves are visible; *b*, remains of aerial shoot. C, corm cut in half vertically; *c*, lateral bud at the side of the withering aerial shoot; *d*, remains of corm of previous season.  $\times 2/3$ .

become firmly anchored in the soil by their lower ends, and then contract at the upper end nearest the corm. This drags the new corm downwards so that a more or less constant level is maintained. Many corm-bearing plants throw up showy flower shoots before the new leaves appear, and are consequently popular in gardens. They include crocuses, gladioli, montbretias and many other such plants. The swellings of the so-called bulbous buttercup (*Ranunculus bulbosus*) of English meadows are really corms. The meadow saffron (*Colchicum autumnale*), grown for the saffron of its stigmas and the gout-relieving alkaloid of its corms, characteristically bears its new corms at the side (Fig. 112) instead of above the old one, because they originate from lateral buds low down instead of near



its top. Montbretias produce a string of corms one above the other.

When crocuses and similar plants are left in the ground, the new corms must develop where they are and, after a few years, become very crowded. The new plants are therefore apt to become impoverished and feeble. If the corms are lifted out and moved into new soil they are enabled to make better growth again.

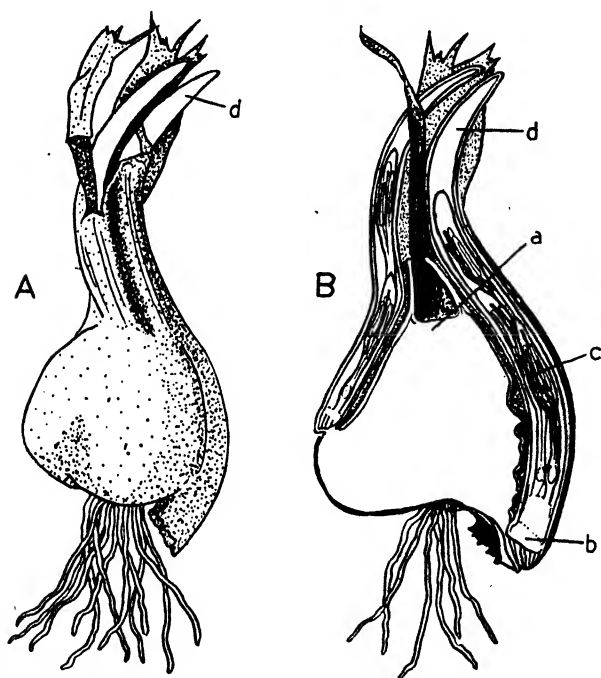


FIG. 112.—Corm of *Colchicum autumnale*. A, surface view. B, cut in half vertically; *a*, scar of aerial shoot; *b*, base of lateral bud; *c*, flower rudiment in lateral bud; *d*, tip of bud.  $\times 3/4$ .

### Bulbs

The life history of a bulb-forming plant is very similar to that of a corm-producing plant. A bulb differs structurally from a corm principally in the fact that it is the scale leaves that swell and accumulate food reserves instead of the stem, which remains a mere shortened-down disc on to which the leaves are crowded (Fig. 113). Outside the massive bulb-scales with the food reserves there is sometimes a layer of membraneous brown scales that protect the bulb from desiccation (Fig. 113 Aa). This is the resting condition of a

bulb, like that of an onion or tulip. It sprouts by means of its apical bud often terminating in a flower sustained by the food reserves of the bulb. The full development of the leaves below the flower comes later, and then the formation of new bulbs begins. They appear as axillary buds in the axils of the scale leaves of the old bulb (Fig. 113 Bb). Several may be formed and their growth soon disrupts the remains of their predecessor. The cycle is subject to the same disadvantage of overcrowding that the corns suffer. Handsome tulips,

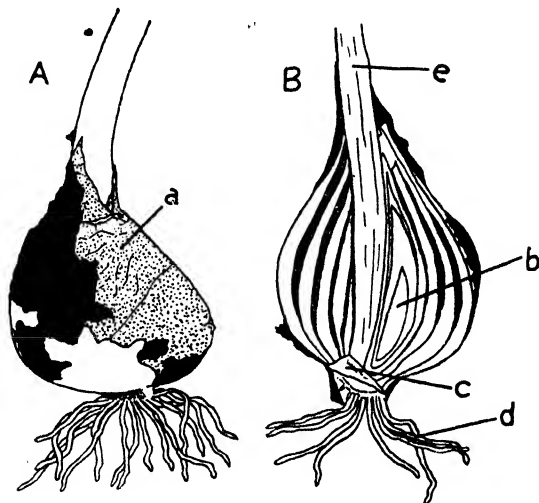


FIG. 113.—Tulip bulb. A, surface view; *a*, outer scale. B, cut in half vertically; *b*, axillary bud; *c*, disc-shaped stem; *d*, adventitious roots; *e*, apical aerial shoot.  $\times 2/3$ .

for example, can only be produced by annual transplanting into renewed soil. Not all bulbs are tunicated like those described above. Lily bulbs (Fig. 114) have no protective outer scale and the food-bearing scales are more loosely arranged and spreading. Such bulbs are not so resistant to unfavourable conditions.

### *Bulbils*

Bulbils resemble small bulbs in their structure, but are borne above ground usually in place of flowers (Fig. 115). They eventually become detached, fall to the ground and strike root from the base.

### *Perennation, Multiplication and Spreading*

Runners, rhizomes, tubers, corms and bulbs all serve to carry on the plant in its vegetative form from one growing season to another ;

that is to say they are primarily a means of perennation. Food is accumulated in them during the season of active vegetation, laid up during the unfavourable season, and is immediately available for growth as soon as conditions are good again. The position of the shoots, on or under the ground, also ensures some measure of protection.

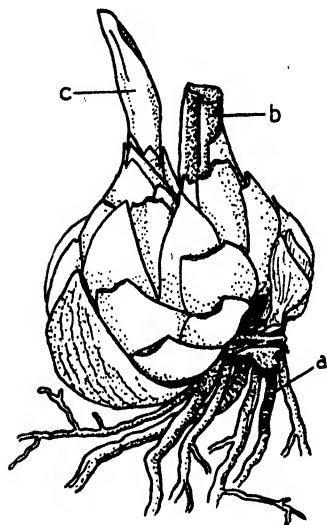


FIG. 114.—Lily bulb in surface view. *a*, contractile root, the wrinkles are due to shortening which drags the bulb downwards in the soil; *b*, withered aerial shoot; *c*, apical bud of bulb on left which originated as a lateral bud of the older bulb behind.  $\times \frac{1}{2}$ .

When a runner rots away between rooted nodes, or a rhizome branches and the old parts die off, new plants are established. A population thus arises by vegetative reproduction (a clone),<sup>1</sup> which consists of parts of an original individual rather than its descendants. Any shoot that has the power of rooting at its base may be regarded as a potential individual capable of separate existence. This is so foreign to the usual idea of the individual that we get from the human race and the higher animals, that it amounts to a major distinction between them and the higher plants. The extensive power of producing new individuals vegetatively results from the relatively low degree of organisation and integration of parts that exists even in the higher plants. As long as a tissue is capable of performing

all the major natural functions, it is capable of independent existence; but when specialisation has gone so far that it depends entirely on neighbour tissues for any of the primary necessities, then the organism can only exist as a whole. This is the stage arrived at in the higher animals; but plants, with their indefinitely prolonged and constantly repeating pattern of branched growth, are not nearly so specialised.

Vegetative propagation, whether by runners or underground shoots, may thus result in multiplication of individuals of a rather special kind. The successful propagation of a species requires not only multiplication but also spreading, since, if the new individuals are not dispersed, they will interfere mutually with each other's

<sup>1</sup> Greek κλών (klōn), a sprout.

growth. The different methods of vegetative propagation differ very much in this. Runners, like those of strawberries, may achieve considerable length and so place the young offsets in advantageous positions for growing; but new corms and bulbs produced on and

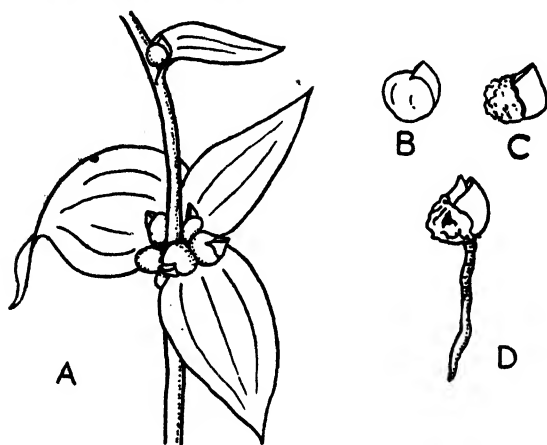


FIG. 115.—Bulbils of *Lilium tigrinum*. A, forming in the leaf axils. B–D, stages of germination.  $\times 2/3$ .

within the old shoots soon become badly crowded. They are usually found in plants growing in extremely dry situations, such as the South African veldt, where growth is very slow at best and thorough protection against desiccation is the prime necessity. Under the

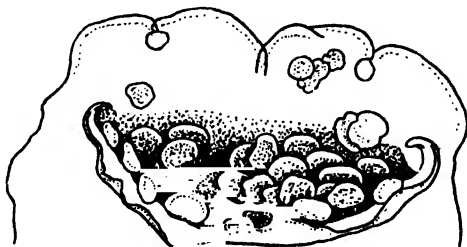


FIG. 116.—*Lunularia*, gemmæ cups. The gemmæ are small detachable pieces of the thallus that grow into new ones.  $\times 25$ .

English climate, which runs to no such extremes, plants with long runners or rhizomes throwing up frequent aerial shoots are more successful, as witness the creeping buttercup and the couch-grass respectively.

Vegetative propagation is by no means limited to the flowering

plants, but occurs freely throughout the plant kingdom. The long, free-floating filaments of *Spirogyra* break up into separate parts, each of which goes on growing. The liverwort *Lunularia* sheds small pieces of the thallus, that grow up into new ones (Fig. 116). Moss stems branch and die away behind leaving free ascending shoots.



FIG. 117.—Young plantlets forming on the edges of an *Asplenium* frond. About nat. size.

Among the ferns, *Asplenium* produces new plants as outgrowths from the edge of the frond (Fig. 117); *Dryopteris* has branching rhizomes and *Pteridium* (Fig. 107 C) is one of the most aggressive of all rhizome-formers. These are only a few characteristic examples of a habit general among plants.

## Practical Work

### ERECT HERBACEOUS ANNUAL

(1) Examine a small herbaceous annual with a single main stem and taproot. Make a sketch showing the following parts: taproot, side roots, hypocotyl, cotyledons if still present, node, internode, foliage leaf, veins, terminal bud, axillary bud, flower bud, flower and fruit if present.

Suitable species easily obtained are *Capsella bursa-pastoris* (Shepherd's purse), *Stellaria media* (Chickweed), *Brassica sinapis* (Charlock), or any garden annual such as *Clarkia*, *Godetia*, *Iberis* (Candytuft) or annual *Delphinium*.

### RUNNERS

(2) Examine a strawberry plant with one or more runners. Note that the runner is produced in the axil of a lower leaf and bears a scale leaf with a bud in its axil. Note also the *offset* (young plant) formed by the apical bud striking roots and turning upwards. This in its turn may have a further runner again produced in the axil of a lower leaf and *not* a continuation of the original runner.

Other plants with runners readily obtained for examination are: *Ranunculus repens* (Creeping buttercup), *Nepeta glechoma* (Ground ivy), *Potentilla reptans* (Cinquefoil).

### RHIZOMES

(3) **Monopodial.** Examine and sketch a rhizome of *Agropyrum repens* (Couch-grass, squitch). The main stem or rhizome is branched and colourless with small, colourless *scale leaves*. Clusters of *adventitious roots* come from the *nodes*. Note the *apical buds* at the tip of each branch continuing the underground growth indefinitely. Each terminal bud is covered with sharp, pointed scale leaves which assist penetration of soil or even of foreign tissues encountered, such as potatoes. Note the *lateral branches* also produced at the nodes. They are green with fully expanded and normal leaves above ground.

(4) **Sympodial.** Examine and sketch a rhizome of *Iris*. This is slow growing, thick and glutted with abundant carbohydrate. Note the numerous *adventitious*

roots and the scars where leaves have been attached extending almost completely round the rhizome. The dots show where the veins were sealed off. Towards the apex a cluster of green aerial leaves will still be attached. The constrictions of the rhizome mark the limits of a single season's growth. Note how the old rhizome rots away behind. The terminal bud eventually becomes a flower bud, turns upwards and grows above ground. Note the lateral bud in the axil of the leaf which will continue the growth of the rhizome.

## TUBERS

(5) **Chinese Artichoke.** Sketch the thickened branching rhizomes of *Stachys tuberifera*. Note the thin lengths of rhizome preceding and following the tuberous parts. Observe the constricted nodes with triangular scale leaves and axillary buds in opposite pairs and note that they alternate at succeeding nodes. Mark the upturned terminal bud.

(6) **Potato. Dormant stage.** Examine a potato newly dug, or at least before it has sprouted. Mark the scar of the stalk now withered away, the terminal bud at the far end and the lateral buds, or eyes, inserted on a spiral, and the minute ridges below the eyes which represent the insertion of scale leaves. Cut in half longitudinally; note the internal parenchyma glutted with starch (smear with a little iodine solution), the vascular strands running to the eyes and the corky insulating layer over the surface.

(7) **Potato. Sprouting stage.** Examine a seed potato ready for planting. (This can only be done during spring and early summer.) Note the sprouts (young shoots) developing from one or more of the eyes, with their apical buds, scale and transitional leaves and cluster of adventitious roots.

## CORMS

(8) **Crocus. Dormant stage.** Carefully peel off the dry, membraneous scale leaves and note that they extend right round the swollen stem. They are inserted at successive levels (nodes) and overlap one another. Note the brown circular scars left when they are pulled off.

Identify the broad scar at the base of the corm where it was attached to the previous year's growth, and the circle of root rudiments around it. Identify also the stem scar at the apex of the corm. This may be almost obliterated by the growth of a nearby lateral bud. Several others may also be present, all in the axils of the scales. Cut the corm longitudinally with a sharp knife, taking care to pass through the terminal scar and through one of the lateral buds near the apex. Within the bud note the external scale leaves, rudiments of foliage leaves and one or more flower buds. Note the parenchyma of the corm itself, glutted with starch (test with iodine), and the vascular strands running from the base towards the nodes.

(9) **Crocus. Flowering stage.** Compare the flowering stage, when one or more, of the lateral buds has grown up to produce flowers and leaves, with the above. Note the swelling at the base of the aerial stem, the beginning of a new corm.

## BULBS

(10) **Tulip. Dormant stage.** Cut the bulb longitudinally through the centre. Note the disc-shaped stem at the base with its attachment scar to the old bulb below and the ring of root rudiments around it. Above are attached the outer membraneous scales, the fleshy bulb scales and the terminal bud. Note that this already consists of foliage leaves and the flower. Look also for one or more small buds on the axils of the bulb scales. These are the precursors of new bulbs.

Crush and extract the bulb scales under water. Filter the extract and test aliquots for starch, reducing and non-reducing sugars (p. 83).

(11) *Tulip. Flowering stage.* Examine an early tulip plant. Note that the roots have now grown out from the edge of the stem. Cut the bulb longitudinally and note the flabby and depleted condition of the old bulb scales and the growth of new bulbs from the axillary buds. Observe the foliage leaves borne on the stem below the large terminal flower.

#### ROOTSTOCKS

(12) Examine a dandelion plant and sketch the thick *taproot* dividing into branches below and containing abundant reserves; the thinner *lateral roots* and the clusters of *foliage leaves* borne on one or more short stalks at the top of the root.

## Chapter XV

# TISSUE ELEMENTS OF THE SEED PLANTS

All the various elements that make up the tissues of the vascular plants are derived from meristematic cells such as are found at stem and root apices. They have already been described on page 48. These cells differentiate in many different ways during growth, giving rise to a large variety of permanent forms. The ground tissue forming most of the softer parts of plants is composed of parenchyma, whose cells develop from the meristems by comparatively simple transitions. They have been described on page 47. The green cells of leaves (p. 64) are a particularly important form of parenchyma on account of their plastids containing chlorophyll. Many of the adult cells of the higher plants differ in one way or another from the parenchyma type, and a few of the more important variations are described in this chapter. It will make the study of the organs and tissues of the higher plants easier to know something first of the principal cellular elements of which they are made up.

### *Secretory Cells*

Secretory, or glandular, cells remain densely filled with protoplasm even when adult. They may have vacuoles, but these occupy a relatively small part of the cell. The nucleus is usually conspicuous and the cell wall remains thin. Secretory cells resemble the glandular epithelial cells of animals and have a similar function. They retain an active metabolism that becomes specialised for the production of some particular substance varying with the cells in question. Thus the nectaries of flowers consist of groups of surface cells which produce and secrete nectar, a mixed solution of sugars. The glands of insectivorous plants (Fig. 118 C) secrete proteolytic enzymes capable of dissolving the proteins of their victims' bodies. Glandular hairs (Fig. 118 A) secreting various sticky solutions are common on the younger parts of plants. Glandular cells secreting resins line the



walls of internal resin ducts (Fig. 118 B), and those secreting etherial oils often open into special internal cavities.

### Storage Cells

The tissues of bulb-scales and other swollen organs described in the previous chapter are composed very largely of storage cells. These usually resemble normal parenchyma in having thin cell walls and large vacuoles with a thin layer of cytoplasm between. In an extreme form the vacuole becomes much swollen by the accumula-

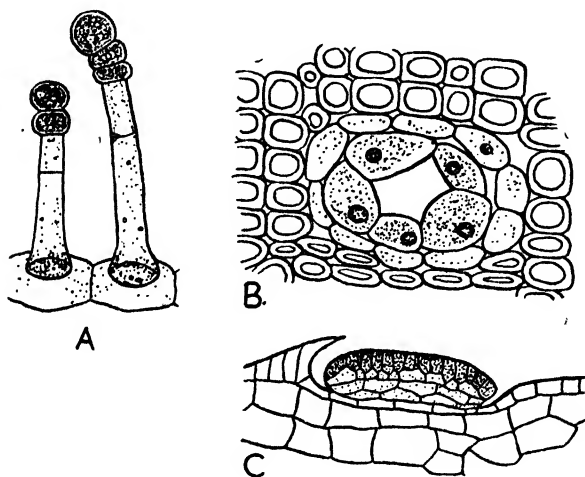


FIG. 118.—Secretory cells. A, glandular hairs from belladonna flower.  $\times$  about 300. B, resin duct lined by glandular cells in the stem of *Pinus austriacus*. C, gland on the inner surface of a *Nepenthes* pitcher.

tion of dilute watery sap, and the tissue may be regarded as a reservoir or water-storage tissue. The internal tissues of succulent plants are of this kind almost entirely. In beetroots (Fig. 119), carrots and similar tissues the sap accumulates very high concentrations of sucrose—up to 20 per cent. in sugar-beet—and so becomes a store of food as well as of water. The general form of the cell remains similar to that of water-storage cells. If the stored substance is a solid or gel like starch or protein, the whole cavity of the cell may eventually be filled by it, and detection of the protoplasm which produced it becomes very difficult. The protoplasm may even die away when accumulation is complete. Familiar examples are the starch-containing cells of potatoes (Fig. 34, p. 76), and the cells of the reserve tissues of seeds. Starch and protein-storing cells from a barley grain

are shown in Fig. 38, p. 81. Fats are stored within the protoplasm of some cells as droplets (Fig. 36, p. 78). A different type of storage cell altogether is found in lupin seeds and date stones. Labile hemi-



FIG. 119.—Cells of red beetroot showing small nuclei and thin cytoplasmic lining. The cell is almost completely occupied by the sugary solution of the vacuole.  $\times$  about 300.

celluloses, capable of being redissolved by the cell enzymes, are deposited in the cell wall, which becomes much thickened in consequence (Fig. 35, p. 77).

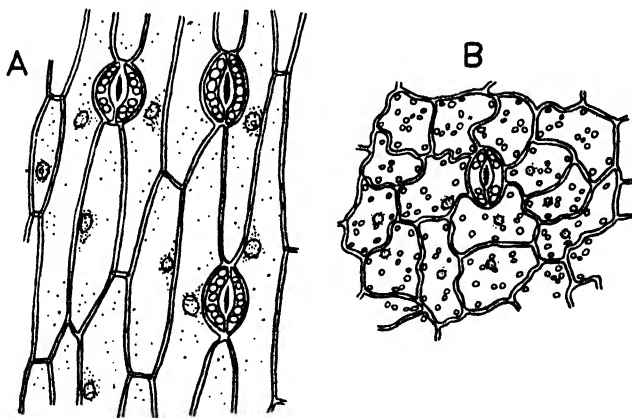


FIG. 120.—Epidermal cells. A, *Agapanthus umbellatus*, strap-shaped leaf with cells elongated in long axis of leaf. B, *Lonicera periclymenum* (honeysuckle), broad leaf, epidermal cells with wavy vertical walls. Note the scattered chloroplasts. The specialised cells are the guard cells of the stomata.  $\times$  about 200.

### Surface Cells

The surface layer of cells of stems and roots is directly exposed to the air on its outside, and shows characteristic properties associated with this fact. To begin with the cells are closely fitted together

without intercellular spaces, forming a continuous skin. They are usually somewhat elongated in the same direction as the organ of which they are a part. The epidermal cells of broad leaves usually have a wavy outline when seen in surface view (Fig. 120 B), because the walls go on extending after cell enlargement has stopped. The outside wall itself is covered with a cuticle, a thin layer of cutin (see Fig. 37, p. 79) developed *outside* the original cellulose layer at a very early stage. This insulates the cell from the atmosphere and retards water loss. Epidermal cells thus come to have something of the nature of water-storage cells which they also resemble in their general structure.

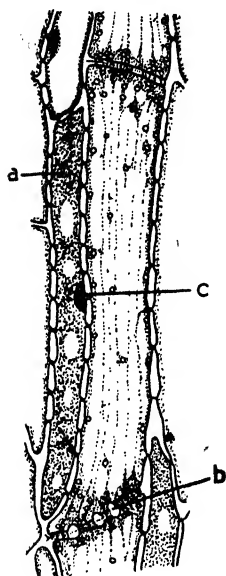


FIG. 121.—Sieve-tube and companion cell from stem of *Nicotiana tabacum*. *a*, cytoplasm of companion cell; *b*, sieve plate; *c*, nucleus. After Crafts.

### Conducting Cells

(*a*) *Sieve-tubes*. Food transport appears to take place in the vascular tissues of higher plants in chains of elongated cells comparable with the chains of elongated medullary cells of *Fucus* (p. 129). The name sieve-tube is applied either to the chain as a whole or to the individual cells composing it. In the angiosperms the most typical form of sieve-tube cell is several times as long as broad and has cross walls at either end, the *sieve plates*, which are perforated by numerous comparatively large holes passing right through from one cell cavity to the next, a most unusual arrangement (Fig. 121). The side walls are slightly thickened and have thin places, or pits, in which the first-formed layer, the

middle lamella, remains as a separation from the adjacent cells. In surface view these pits are seen to be collected into groups or lattices (Fig. 122). In some species the perforations of the sieve plate are similarly collected into lattices.

The cytoplasm of the sieve-tube is a thin layer containing occasional plastids and starch grains and surrounding a large central vacuole. It joins with the cytoplasm of the next sieve-tube through the open pores of the sieve plate, but opinion is divided as to whether the vacuoles are continuous also or whether the pores are fully occupied by the cytoplasm itself. Mature sieve-tubes no longer have

a nucleus in their cytoplasm, and are the only example known of plant cells in such a state. It is perhaps to be explained by their relations with their *companion cells*. The sieve-tube mother cell, while still in the meristematic stage, cuts off one, or sometimes more,

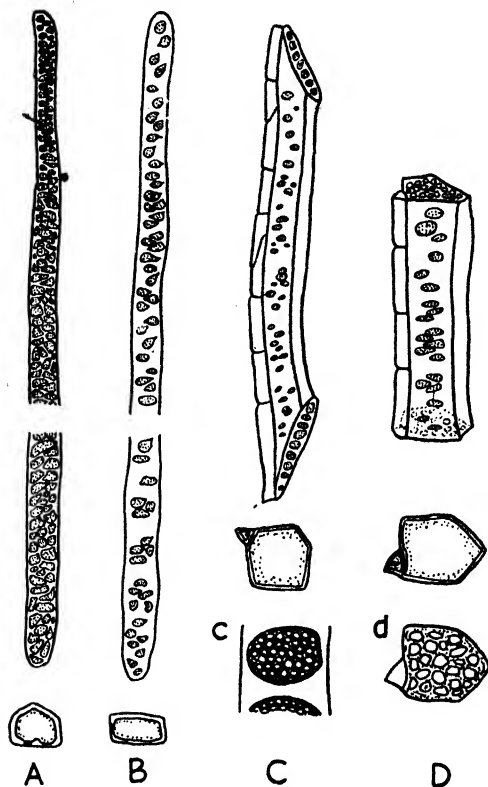


FIG. 122.—Sieve-tubes. A, *Pteridium aquilinum* (a fern), only one quarter of the sieve-tube is shown. B, *Tsuga canadensis* (a gymnosperm), one third shown. C, *Liriodendron*; c, detail of sieve plate. D, *Robinia pseudacacia*; d, detail of sieve plate. Side view above and cross section below. C and D show companion cells. After Eames and MacDaniels.

cells before its nucleus finally degenerates. The sieve-tube cell vacuolates and enlarges, especially lengthwise, but the side cell remains narrow and filled with dense protoplasm. It may lengthen or divide, horizontally, into a series of cells, each with abundant cytoplasm and conspicuous nucleus, and remains closely appressed to the sieve-tube partner (Figs. 121 and 122). The cytoplasm of the sieve-tube remains in direct contact with the protoplasm of the companion cells by

means of fine fibres passing through the pit membranes of the lattices on the side walls. The influence of the companion cell nucleus may therefore extend to the cytoplasm of the sieve-tube which has no nucleus of its own.

The thin cytoplasm of the sieve-tube is very easily plasmolysed.

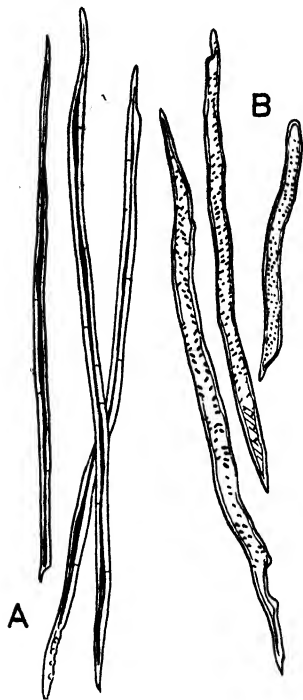


FIG. 123.—Mechanical elements from oak wood. A, fibres. B, fibre-tracheids or "substitute fibres" with small slit-shaped pits.  $\times$  about 100.

It then comes away from the side walls, but not from the sieve plates through which it passes in comparatively coarse strands. The very characteristic plasmolysis figure that results is more easily and more often observed than the natural living state of the cell, because plasmolysis occurs so readily in making a microscope preparation. The shrunken vacuole often has a solid appearance, the so-called slime strand, which results from the coagulation of its soluble proteins. During the normal life of the cell these proteins are in solution in the vacuole and perhaps in course of transit. Towards the end of the active season, carbohydrate deposits are often laid down over the sieve plates and apparently reduce, or entirely stop, all transport through the sieve-tubes. The blockage may be permanent, or may later be removed by the disappearance of the carbohydrate callus pad.

This is the form taken by sieve-tubes in the true flowering plants, the angiosperms. A different pattern is found in the gymnosperms (Fig. 122 B). The individual cells are much longer and have no specialised cross walls but just rounded off endings. Their side walls have sieve lattices scattered over their entire length. *Dryopteris* has similar sieve-tubes with even more abundant lattices (cf. Fig. 122 A). Transitional forms between this condition and the more highly specialised one described above are found in some angiosperms. An example is shown in Fig. 122 C.

The sieve-tubes are commonly supposed to be the main conducting

channels of food substances, i.e. nitrogenous substances (soluble proteins, amino-acids and amides) and sugars. We know very little of the manner in which the transport takes place, though removal of

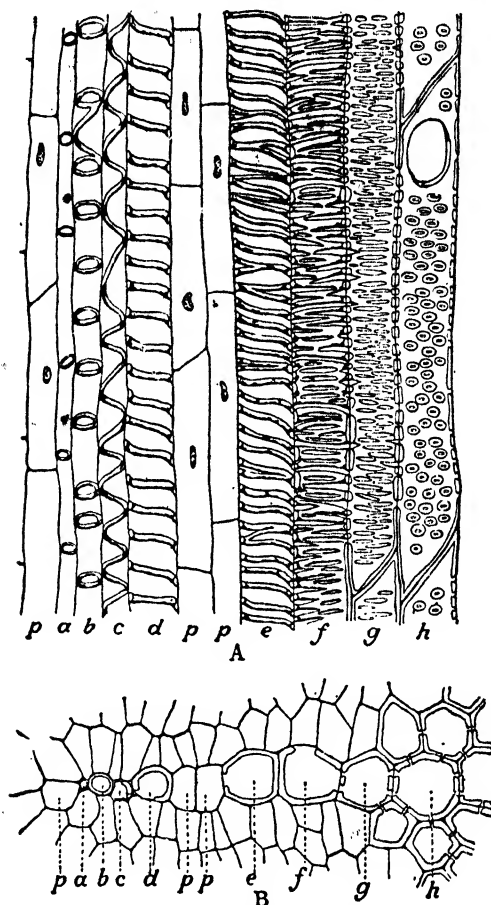


FIG. 124.—A, longitudinal section of water-conducting elements, B, transverse section to correspond; *a*, annular elements greatly stretched by elongation of the stem; *b*, annular element differentiated later and not so much stretched; *c* and *d*, spiral elements. On account of their great length it is difficult to be sure whether these are parts of tracheids or of vessels; *e* and *f*, reticulate elements; *g*, scalariform; *h*, pitted vessel, note the opening into an adjoining element near the top; *p*, parenchyma. After Eames and MacDaniels.

the phloem, the tissue containing the sieve-tubes, brings food conduction to a standstill; and makes it fairly clear that the sieve-tubes are the path of transport.

(b) *Tracheids* (Fig. 124). A tracheid is a cell that has become adapted to water conduction. It is developed from a meristematic cell by vacuolation and a degree of lengthening that in young organs like rapidly growing root tips may be astonishing. While this is going on the cell wall is thickened and *lignified* (p. 209) more or less uniformly in tracheids that do not elongate excessively, but in definite patterns in others. When the wall thickening is complete, the protoplasm dies leaving a cell cavity filled with water, which is in communication with that of adjacent tracheids without any interruption by semipermeable membranes. Different sorts of tracheids

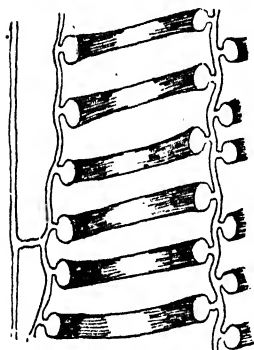


FIG. 125.—Part of a spiral element very highly magnified and seen in longitudinal section showing the narrow attachment of the spiral band to the thin wall.

may be recognised according to the thickening pattern on their walls:

(i) *Annular tracheids* (cf. Fig. 124 (a) and (b)) have their thickening in the form of rings. When the cell is young they are close together, but as it becomes longer they become further and further separated. In Fig. 124 the tracheid (a) is at a more advanced stage of development than (b).

(ii) *Spiral tracheids* (cf. Fig. 124 (c) and (d)) have one or more lignified bands laid down on the inner surface of the wall (Fig. 125) running round and round the cell through its entire length. Like the rings of annular tracheids, the turns of the spiral are at first close together, but become drawn out as elongation and stretching of

the thin parts of the wall continues. The composition of the thin areas remains unchanged. Both annular and spiral tracheids are formed in organs (such as root tips) that are still rapidly elongating, and they continue to be passively stretched after their protoplasm is gone.

In the following types the wall thickening is more abundant and more rigid; they are typically differentiated in tissues that are becoming thick and woody and whose stretching is done.

(iii) *Reticulate<sup>1</sup> tracheids* (cf. Fig. 124 (e) and (f)) have a network of thickenings, which may consist of spirals with more or less numerous cross links. In (iv) *Scalariform<sup>2</sup> tracheids* (cf. Fig. 124 (g)) the unthickened portions of the wall are reduced to isolated elliptical islands between horizontal bars of thickening suggesting the appearance of a ladder. Finally, there are (v) *Pitted tracheids* in which the

<sup>1</sup> Latin *reticulus*, a net.

<sup>2</sup> Latin *scalae*, a ladder.

thickening is continuous all over the substance save for small areas, the pits, that are commonly of the bordered type described below.

(c) *Vessels* (Fig. 126). Vessels have the same functions as tracheids and develop in a similar way. Instead of being single cells, however, they consist of a row of cells with open communication between them. This is due to the dissolving away of the end walls in

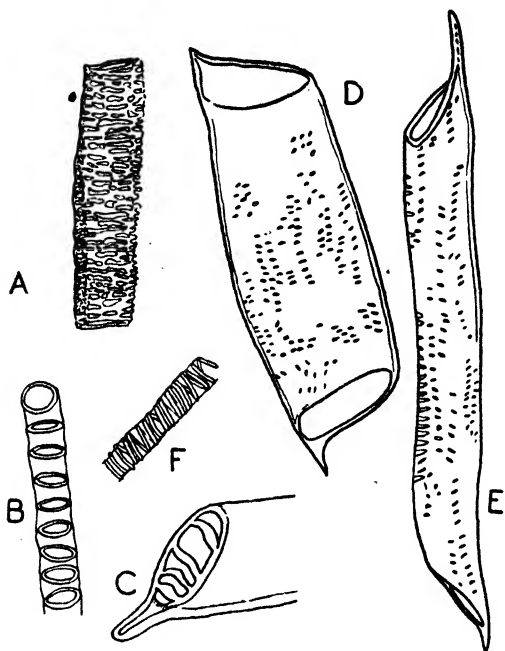


FIG. 126.—Vessels. A, part of a reticulate vessel from *Cucurbita* stem. B, annular vessel from the same. C, vessel-ending from *Rhizophora* (mangrove) showing bars still remaining across the opening. D and E, vessel segments from oak wood. F, part of spiral vessel from *Cucurbita* stem. All drawn to the same scale.  $\times 130$ .

part or altogether, while the protoplasm of the cells is still active. The individual vessel segments may be long, like tracheids, or short and wide. The widest tracheids are not much more than  $100\ \mu$  in diameter and most are much less; while vessels commonly reach a width of  $300\ \mu$  and some, e.g. in vines, measure as much as  $700\ \mu$  across. In vines also the vessels may run for many metres without any cross walls at all, but in most woods occasional cross walls occur more frequently. In sycamore they occur on the average about once in 10 cm., equivalent to a run of perhaps 50–100 cells. Vessels have the same types of thickening and pitting as tracheids.



They are found only in the angiosperms; the water-conducting tissues of gymnosperms, ferns and other vascular plants consist of tracheids only.

### *Mechanical Cells*

Mechanical tissues are those that give strength to a bulky plant and enable it to stand erect and spread its leaves and branches in the air. This results from more or less massive layers of thickening laid down on the walls of their cells. Pitted tracheids, with their heavy walls and comparatively small cavities, may be regarded as mechanical as well as conducting cells, especially when they are formed in great masses as in the wood of tree trunks (Fig. 123 B).

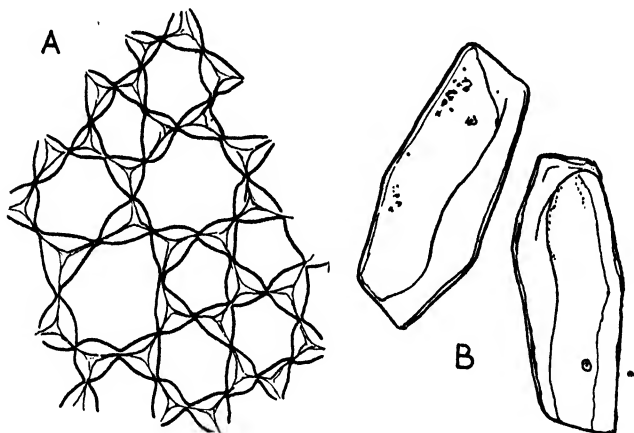


FIG. 127.—Collenchyma from the stem of *Cucurbita pepo*. A, transverse section. B, isolated cells showing bands of cellulose thickening down some of their long walls.  $\times$  about 300.

(a) *Collenchyma Cells*. Collenchyma is a tissue found near the surface of young stems and in the petioles and midribs of leaves. Its cells (Fig. 127) are elongated in the long axis of the organ of which they are a part and are characterised by irregular heavy thickenings of cellulose, especially as vertical bands at the cell corners. They retain their protoplasm alive even when mature. Collenchyma imparts a tough and leathery strength owing to the elastic nature of cellulose.

(b) *Fibres*. Fibres develop into long, narrow cells when mature, with tapering and overlapping ends (Fig. 123 A). The protoplasm dies when the cell is mature, and the cavity may be reduced almost

to nothing. The walls are penetrated, except at the middle lamella, by simple pits, much narrower than the bordered pits of tracheids. During the life of the protoplast they are occupied by protoplasmic fibres and are probably the path by which food materials for the building of the wall-thickenings enter. Fibres are commonly found in masses rather deeper seated than collenchyma, but still not far from the surface of stems, petioles and midribs. They also form a large part of the wood of trees. They give a tough but usually rather more rigid strength than collenchyma, because their walls are lignified (p. 209). Fibres are the basis of many important materials such as

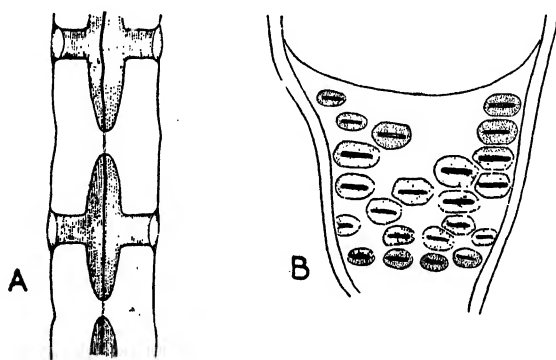


FIG. 128.—Bordered pits in vessels of sycamore stem. A, in longitudinal section showing the thin middle lamella in black and the slightly funnelled pit cavities. B, surface view of a piece of the wall near the end of a vessel. The cavities of the pits are injected with a dye. Note the menisci in A. Very highly magnified. After James and Baker.

wood, rope, newsprint and sacking. Non-lignified fibres also occur, e.g. in flax and are the source of linen and the best grades of paper. Their special combination of toughness and elasticity is still unrivalled. No other material can be spread so thin and remain as untearable and chemically resistant as a good paper.

### *Pits*

The thickening of cell walls is often interrupted by pits where the original wall formed at cell division, the middle lamella, is not added to. Pits are always formed opposite one another in adjacent cells of a thick-walled tissue, so the cell cavities are only separated at these places by part of the middle lamella, the pit membrane. *Simple pits* are usually circular in section appearing as lighter circular areas when the wall is seen in surface view. Their walls are commonly perpen-

dicular to the middle lamella, and the pit is of equal diameter all through. *Bordered pits*, named from their appearance in surface view have comparatively wide areas at the pit membrane, but become narrower as thickening of the wall goes on (Fig. 128 A). The cavity thus formed in the wall appears dimly as a border surrounding the actual pit opening. The opening itself may be round or slit-shaped (Fig. 128 B). When the pits are closely crowded together, their outlines become hexagonal instead of circular (Fig. 128 B). The tracheids of gymnosperms, like *Pinus*, have single rows of large bordered pits on their sides. The pit membrane is thickened at the

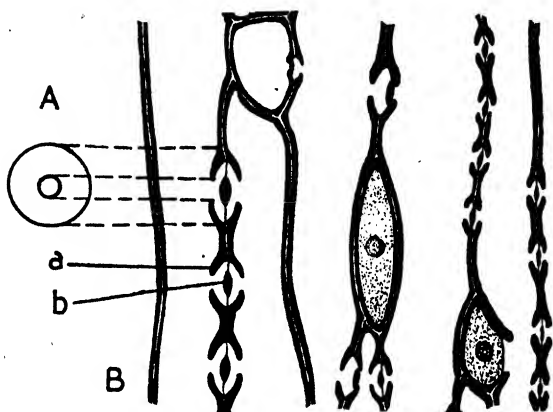


FIG. 129.—Bordered pits in the tracheids of *Pinus* stem. A, surface view of a single pit. B, parts of tracheids in longitudinal section; a, bordered pit; b, thickened torus on the middle lamella. Semi-diagrammatic.

centre into a torus (Fig. 129) and the surrounding unthickened middle lamella is said to be perforated with actual holes.

The fine threads of cytoplasm connecting the protoplasts of adjoining cells are sometimes, though not always, confined to the pit membranes of thick-walled cells. We do not know what determines the formation of a pit at any given spot in the cell wall. The deposition of cellulose and other thickening materials is not bound to be of advantage in all instances. It may result from an excess formation of carbohydrates when photosynthesis is unchecked, but the supply of nitrates and other salts is inadequate for the formation of enough protein for new cells. Most plants living in dry climates with abundant light form great masses of thick-walled tissue, not all of which is mechanically useful.

*Materials of the Cell Wall*

The fashion of referring to the substance of unmodified cell walls as cellulose is very inexact. Very few walls consist of anything like pure cellulose, cotton hairs being the most notable example. The middle lamella (p. 57) is composed of pectic materials (p. 78) and in a mature tissue acts as a sort of cement holding the cells together. It can be dissolved in a solution of ammonium oxalate and, when this is done, the cells of the tissue fall apart (Fig. 130 A). The thickening layers that are deposited on the middle lamella as the cells grow and differentiate usually contain about 50 per cent. true cellulose. The other half consists of mixed carbohydrates, the hemicelluloses (p. 77). There may also be small quantities of pectic substances and

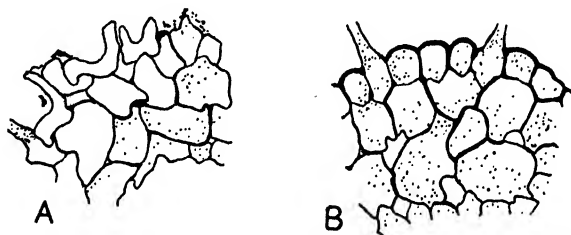


FIG. 130.—A, piece of the cortex of chinese cabbage root immersed in ammonium oxalate solution. The cells are falling apart owing to solution of the middle lamella. B, similar tissue recovered after transfer to tap-water containing calcium.  $\times$  about 200. After Cormack.

other "impurities." This composition becomes much changed when elements such as tracheids and fibres are formed.

*Lignification*

Lignification is the essential feature of wood formation, the valuable technical properties of wood resulting very largely from the nature of lignin deposited in the walls. In spite of the stimulus thus given to its study, the chemistry of lignin is still largely unknown. It gives well-marked colour reactions with phloroglucin and aniline compounds which makes its detection easy (Exp. (11), p. 212). Its presence has important results upon the physical characters of cell walls; it makes them stiffer and more capable of withstanding crushing and bending strains without decreasing their permeability to water. Of a fully lignified cell wall, about one-quarter is lignin, one-half cellulose and the remaining quarter a mixture of hemicelluloses, pectic and other substances.

### *Cutinisation*

Cutinisation is a change limited to the outer walls of surface cells. It consists of the formation of a layer of cutin, deposited outside the cellulose layer of the wall. An intermediate layer, part cellulose and part cutin, is also sometimes formed. Cutin is a fatty substance. Probably fatty acids permeate outwards from the cell and become oxidised and condensed in contact with the outside air, and so form a sort of skin. The process is akin to the drying of a varnish. The fatty nature of cutin is revealed by its power to take up fat stains, such as Sudan III, when warmed. Physically it is highly impervious to water, as would be expected from its fatty nature.

### *Suberisation*

Suberisation is a change somewhat akin to cutinisation. Suberin is probably a name for a mixture of complex substances also derived from fatty acids like cutin. Unlike cutin, it is laid down in zones included within layers of cellulose, though not impregnating it like lignin. Suberised cells form an impervious layer over the shoots of woody plants and are described more fully on page 273. The bottle corks of daily use are pieces of bark cut from the cork oak, which produces this tissue in unusual thickness. They owe their value to the imperviousness and resistance to chemical breakdown of suberin.

### *Mucilage Formation*

Many of the cell wall constituents, e.g. the hemicelluloses and pectic substances, are closely related to mucilages and, in certain circumstances, mucilages are formed from them. The wall then takes up and retains much larger amounts of water. It consequently swells up and tends to form a sol instead of a coherent gel. The middle lamella is particularly liable to this change, and all the medullary mucilage of *Fucus* is formed thus. The mucilages formed by some of the red seaweeds, *Chondrus* and *Gigartina*, are the source of agar, an important medium in bacteriology and an ingredient of some table jellies. Similar changes occur in the cells of higher plants, such as the swelling of linseed walls when wetted (Exp. (17), p. 212) and the lubrication of the root tip by the mucilage of the root-cap walls.

## **Practical Work**

### **GLANDULAR CELLS**

(1) Strip off a piece of epidermis from the *young* stem of one of the following plants. Mount in dilute glycerine and examine under the microscope. Note the *glandular hairs* of thin-walled cells with conspicuous cytoplasm and nuclei.

Any of the following are suitable: *Petunia*, *Nicotiana*, tomato, *Pelargonium* (garden geranium), black currant (leaf).

(2) Cut a longitudinal section through the fork of a young bracken frond. Mount in dilute glycerine and examine under the microscope. *Glandular cells* will be seen lining a cavity (an *extrafloral nectary*) which opens to the outside through a pore. It may be necessary to make several cuts to get a good result.

If available, examine prepared sections through a floral nectary and the inner surface of a *Nepenthes* pitcher.

#### STORAGE CELLS

(3) *Sugar*. Cut sections of tulip or onion bulb scales, or beetroot. Mount. Note the large *central vacuole*, *thin walls* and *conspicuous protoplasm*. Put one or more thickish sections into a watchglass and cover with Fehlings solution. Warm for about five minutes, taking care that the solution does not dry up. Add more Fehlings if necessary. Cool. Transfer the watchglass to the microscope stage and examine under the low power. Grains of cuprous oxide will be found in and around the cells, showing the presence of reducing sugars. If the section is first heated with dilute acid, the reaction will be stronger, but the sugar will have escaped almost entirely from the disrupted cells.

(4) *Protein*. Cut transverse sections of wheat or barley grains and soak for half an hour in alcohol. Then transfer to a microscope slide, mount in Millon's reagent and warm cautiously without allowing to dry up. Add more reagent as necessary, then cover and examine. The abundant *reserve proteins* of the *aleurone layer* will be stained red. Draw one or two cells. The initial soaking in alcohol removes aromatic substances which also react with Millon's reagent.

(5) *Starch*. For starch-storing cells see Exp. (3), page 83.

(6) *Water*. Examine the *thin-walled tissue* forming the bulk of any succulent leaf (*Sedum*, *Crassula*, *Sempervivum*, etc.). Contrast with the layer of *tissue near the surface*, containing *chloroplasts*.

#### SURFACE CELLS

(7) Strip pieces of the *lower epidermis* from any of the following leaves by tearing sharply across the veins. Mount in dilute glycerine, examine under the microscope and draw a small group of cells, noting the *thin side walls*, *nuclei*, *thin cytoplasm*, large *vacuoles* and very occasional *chloroplasts*. At least one leaf from (a) and one from (b) should be examined. (a) Iris, onion (inner surface of scale), lily; (b) *Dahlia*, *Fuchsia*, privet, apple, potato, lettuce, ground ivy, *Tropæolum*, snapdragon, sow thistle.

(8) Cut a vertical section of a box or cherry laurel leaf. Mount in dilute glycerine. Examine each of the *epidermal layers* under the microscope and draw one or two cells. Both these leaves have very thick *cuticles*. Leaves with thin cuticles are difficult to cut neatly. Mount a section in chlor-zinc-iodine and note at once the blue staining of the *side* and *bottom walls* and of the *inner layer* of the *outer wall* (cellulose). The *outside layer* stains yellow (cutin).

#### CONDUCTING CELLS

(9) *Sieve-tubes and Companion Cells*. The observation of sieve-tubes in the natural, living condition is very difficult and requires elaborate technique. The characters of the *walls* and *sieve plates* may be examined in longitudinal sections of *Cucurbita* (vegetable marrow) stems. Permanent preparations stained with light green are perhaps the best, but fresh sections will show a good deal. Note the "*slime strand*" (cf. p. 202). Cut transverse sections and examine for surface view of *sieve plates*. Examine also macerated material (see below).

(10) **Maceration Technique.** This is useful for freeing the more resistant elements from other cells to enable them to be examined in the solid. Take small pieces of marrow stem or celery stalk and boil them in water until they are soft. This dissolves the middle lamella and the individual cells can then be teased apart. To do this, transfer small pieces of the softened tissue to a drop of water on a slide and disintegrate with a pair of mounted needles. More resistant stem tissues may be macerated by allowing them to stand for twenty-four hours in 5 per cent. chromic acid.

(11) **Vessels.** Mount some macerated *Cucurbita* tissues in a drop of dilute glycerine and add a drop of aniline chloride solution. Cover. Observe the narrow *annular* and *spiral vessels* and the broader *reticulate vessels*. The thickening will be coloured yellow by the reagent. Look for junctions between vessel segments.

(12) **Tracheids, Bordered Pits.** Cut a longitudinal section of a piece of the wood in a pine twig. Mount in water with a drop of aniline chloride. Examine and draw the *bordered pits* in surface view and in optical section.

#### MECHANICAL CELLS

(13) **Collenchyma.** Cut transverse and longitudinal sections of one of the following stems. Mount in dilute glycerine and draw a group of cells from the outer cortex showing the irregular cellulose thickenings of the walls. The following are convenient; potato, burdock, dead nettles, *Salvia* spp., celery (petioles).

(14) **Fibres.** Examine specimens of macerated willow wood mounted in aniline chloride solution. It consists mainly of *fibres*. Note the thick *walls*, tapering *ends*, simple *pits* and narrow *cell cavities*. Some *vessel segments* with close-set *bordered pits* where they abut on one another will also be present. In a longitudinal section of willow wood, notice how the tapering ends of the fibres are interlocked.

#### MODIFICATIONS OF THE CELL WALL

(15) **Lignification** has been seen in Exp. (11), (12) and (14) above.

(16) **Cutinisation** in Exp. (8) above.

(17) **Mucilaginous Walls.** Examine a dry seed of flax (linseed). Note the sharp outline. Put the seed in a watchglass with water. Its outline is soon surrounded by a transparent fringe. Compare the feel of the dry and the wet seed between the fingers. Compare similarly the feel of *Spirogyra* and *Cladophora* tufts between the fingers. *Spirogyra* has mucilage on its cell walls and *Cladophora* has not. *Cladophora* is the rough, pale scum frequently found on stagnant ponds.

(18) Examine a dry section of flax seed under the microscope; then run on a dilute solution of methylene blue. Watch the swelling of the **mucilage** which will also be stained blue.

THE GROWING POINT OF THE SHOOT

The apex of the shoot is occupied by a bud. This consists of young leaves overarching and protecting the top of the stem, the extreme tip of which is the meristem from which all the tissues of the shoot, both leaf and stem, are developed. It is slightly domed and on its

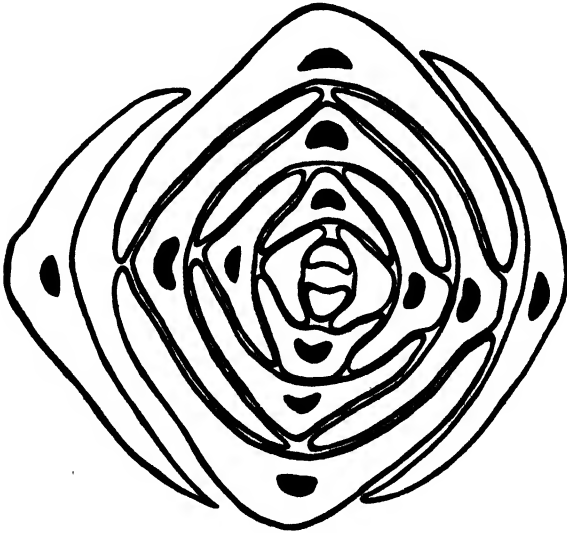


FIG. 131.—*Ligustrum vulgare* (privet), transverse section of the apical bud just above the stem apex, showing the alternating arrangement of the paired leaf primordia.  $\times$  about 50.

flanks arise ridges of tissue which are the beginnings, or primordia, of the young leaves. The placing of successive primordia may be on a spiral or in opposite pairs according to the species. If the primordia arise in pairs, the second pair is usually placed at 90 degrees to the first, i.e. alternating with it, not directly above it (Figs. 131 and 132).



The young leaves as they grow arch over the tip (Fig. 132) and spread out sideways (Fig. 131) so that a jacket of overlapping layers is built over the apex.

The cellular structure of the apex is most conveniently studied

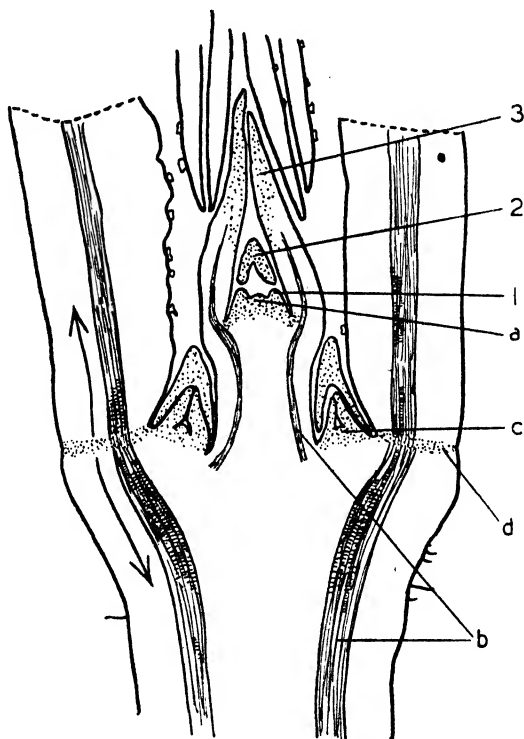


FIG. 132.—*Ligustrum vulgare*, longitudinal section of the stem apex. Meristematic tissues are shaded with dots; vacuolated tissues unshaded. Desmogen strands are shaded with long lines and cross-hatched where differentiation has begun. The arrows show the directions of differentiation, starting in the desmogen at the node; *a*, stem apex; *b*, desmogen strands; *c*, axillary buds; *d*, intercalary meristem at the base of the leaf. 1, 2 and 3, successive pairs of leaf primordia.  $\times$  about 30.

in a longitudinal section passing accurately through the middle of opposite primordia. It must be remembered that only every other pair of primordia is thus seen, and that the alternate pairs exist though they fall out of the plane of the section. They are inserted in the back and face of the sections of stem apparently devoid of primordia. Stems with spirally arranged primordia are still more complicated.

*Apical Meristem*

The dome at the stem apex is constructed of small, closely packed cells with thin walls and no intercellular spaces (Fig. 133). They are completely filled with protoplasm and their nuclei are conspicuous and central. The outer walls in contact with air possess a thin cuticle, which is also continuous over the young primordia and so over the whole surface of the young shoot. The young cells contain oil, some of which passes to the outer surface and is there dried to cutin. The meristem is several cell layers thick and its cells divide from time to

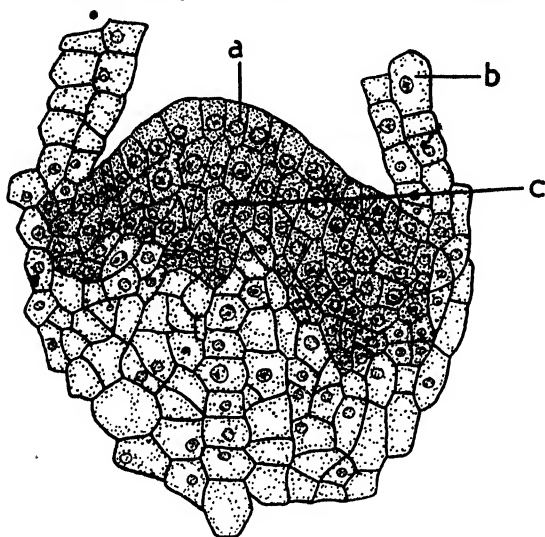


FIG. 133.—Median longitudinal section through the apical meristem of a tomato seedling. *a*, dermatogen; *b*, leaf primordium; *c*, inner cells of meristem.  $\times 560$ . After Whaley.

time, the daughter cells growing to the same size as the surrounding cells. The outermost layer divides only by walls vertical to the surface and so remains one layer deep. It is the origin of the epidermis and therefore called the dermatogen. The deeper-seated meristematic cells divide in all directions, and are the original source of all the internal tissues of the shoot.

The frequent division and growth of the meristematic cells cause them to press against one another. The tissue as a whole does not expand freely because the cuticle is inelastic and so the cells are compressed tightly together. Their shape is determined by this fact since they are fluid droplets surrounded by thin elastic, or perhaps still plastic, walls. They thus tend to pack together tightly with the

minimum of wall surface between them. It has been shown that the ideal figure satisfying this requirement is a tetrakaidekahedron with eight hexagonal faces and six square ones. It is found that "dissected out" meristematic cells have about fourteen irregular faces with four, five, six or more edges. Pentagonal faces are common (Fig. 134). Factors such as unequal growth pressures, unequal cell sizes, gumming together of the cells by the middle lamella, and so on, no doubt account for the degree of irregularity observed in the cell shapes. In the sections of meristems, cells surrounded by others on all sides, and therefore more or less equilaterally compressed, are frequently hexagonal with corner angles approximating to 120

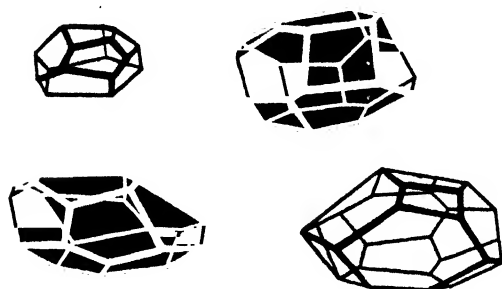


FIG. 134.—Isolated cells from the pith of *Ailanthus*. Starting from the top left, the number of faces shown by each one are 10, 14, 13 and 17. After Hulbary.

degrees. Where a division has very recently taken place, the new wall lies at right angles to the old ones, but as it becomes thickened with cellulose and consequently elastic, the mutual growth pressures force its right angles towards angles of 120 degrees (Fig. 135), with corresponding

readjustment of the neighbouring walls. On the outer surface the inelasticity of the cuticle causes a modification and the outer walls are flattened down instead of being domed as they otherwise would be. The important thing to realise is that the shape of these cells is being determined by physical considerations, such as the incompressibility of their watery contents and the elasticity of their surface walls, not by some obscure strivings of their growth forces after a biological ideal.

#### *Leaf Primordia and Axillary Buds*

The ridges of tissue which are the leaf primordia are covered by the dermatogen which performs numerous divisions in a plane vertical to the surface (anticlinal). These cells remain meristematic and cover the increasing surface by frequent divisions and growth to their usual meristematic size; not by enlargement of individual cells. Below the dermatogen, the next layers of the meristem divide both

anticlinally and periclinally (parallel with the surface). These cells also remain meristematic and fill up the interior of the primordium by means of repeated cell-divisions. Sometimes the primordium has the shape of a papilla, and develops into a leaf with a narrow attachment to the stem by way of a petiole; sometimes the primordium is a ridge (Fig. 136 A) and in the extreme examples found among the monocotyledons that have broad, sheathing leaf bases, a single primordium may encircle the stem more or less completely (Fig. 136 B).

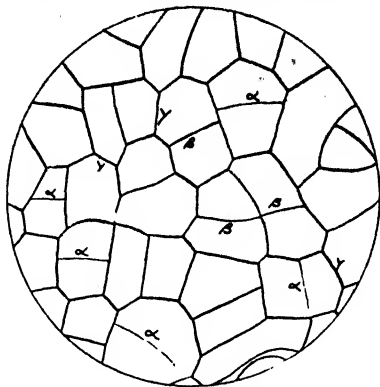


FIG. 135.—Surface cells of a leaf primordium of *Atropa belladonna*.  $\alpha$ , newly formed thin walls;  $\beta$ , slightly older walls beginning to thicken;  $\gamma$ , older walls fully thickened. Note the angles formed where walls of different types meet.  $\times 800$ .

In the axil of the leaf primordium another papilla of meristematic cells may arise even at quite an early stage (Fig. 132 c).

This is the rudiment of the axillary bud, which develops slowly into a lateral meristem similar to the apical meristem just described. It may continue to develop without interruption into an axillary shoot, or it

may become dormant at an early stage of development. Its fate depends both upon internal factors, such as hormones produced by the apical bud, and external conditions. It may even never succeed in developing any further.

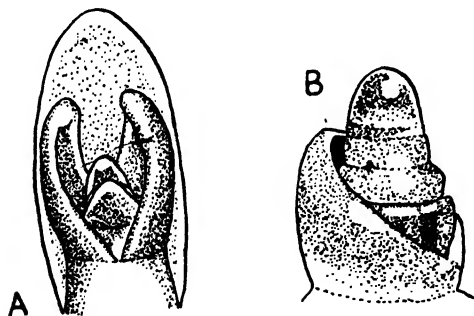


FIG. 136.—Stem apex. A, *Ligustrum vulgare*, internodes elongated. After Priestley and Scott. B, *Agropyrum repens*.  $\times 14$ . After Sharman.

### Development Behind the Shoot Meristem

After a few divisions, when a meristematic cell is beginning to be embedded behind increasing layers of cells above and around it, its rate of division becomes slower and it begins to vacuolate. In Fig. 132 the positions of vacuolated cells are left unshaded.

**Pith.** The cells in the central axis of the stem are generally the first to show this change. They often increase greatly in size owing to the formation of central vacuoles, but usually retain an isodiametric shape not greatly different from that of the meristematic cells. They have been found to have about fourteen sides in the pith of *Ailanthus*, *Asparagus* and *Eupatorium* where they have been counted. They frequently round off at the corners so that intercellular spaces make their appearance (Fig. 137). Although enlargement and turgor of the pith cells still produce some pressure within the tissue (cf. also p. 61),

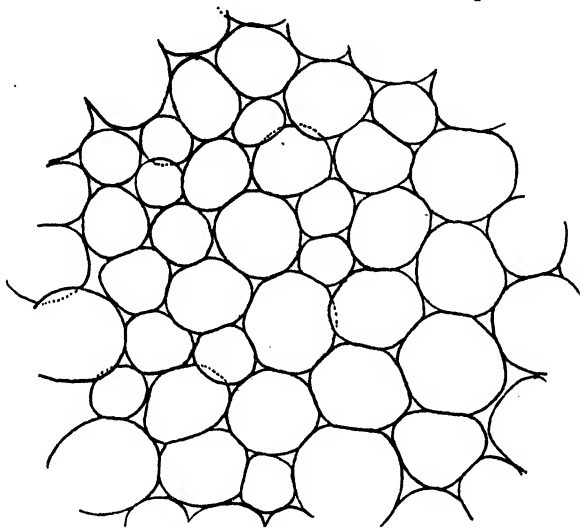


FIG. 137.—Pith cells of *Rumex* sp. showing intercellular spaces.  $\times$  about 250.

it would appear to be less than in the meristematic zones above and outside it. The elasticity of their walls then causes the cells to round off their corners and become more spherical, especially if the cohesion of the middle lamella is not strong enough to hold them together. This is apparently what happens in the young pith. At a later stage the pith cells stop enlarging altogether and, if the outer tissues go on growing as they sometimes do, the pith cells are torn completely apart and a hollow pith is the result.

**Desmogen.** Just outside the pith is the zone which gives rise to the vascular tissue (Fig. 132 b). The cells of this zone remain meristematic much longer than the central cells and divide most often in a plane parallel to the stem axis. Horizontal divisions are rarer, but growth continues so that the cells become elongated though still

retaining all the characters of the meristem. They thus form the desmogen strands, whose cells a little later differentiate into the various elements of the vascular bundles. The first to differentiate are annular and spiral tracheids or vessels which form the protoxylem on the inner side of the desmogen strands while they themselves and their neighbours are still elongating. The thickening bands rapidly lignify and then the protoplasm dies off. This happens first at or just below the node or point at which a young leaf is inserted on the stem (Fig. 132). The differentiation of the protoxylem then progresses in both directions, upwards into the leaf and downwards into the internode below. The strands extend longitudinally down the stem and eventually link up with others and so build a continuous water-conducting system.

### *Elongating Region of the Stem*

The elongating region may stretch for an inch or more behind the meristem. It is the internodes that elongate, carrying the successive leaves farther apart. The nodal regions grow mainly in diameter and their cells do not vacuolate and elongate to the same extent. During the period of elongation the outer tissues of the shoot, following the protoxylem, are also differentiating. The cuticle becomes thicker and the outer layer of the cortex, derived from the meristematic cells just below the dermatogen, frequently becomes collenchymatous (see p. 206) as the cells elongate. Chlorophyll develops in the plastids of the young leaves and cortex and inter-cellular spaces make their appearance in the same tissues.

In the desmogen strands fibres begin to be distinguishable on the outer surface but their walls do not become heavily thickened until elongation is complete. Narrow sieve-tubes (protophloem) usually appear just below the fibres and opposite the protoxylem groups. Other and more complete differentiations only occur after growth in length has ceased.

### **Practical Work**

(1) Pull off the outer leaves from a Brussels sprout, laying them out in order until the apex is almost reached. With a sharp knife or razor cut a longitudinal section through the remaining axis, passing through the tip as accurately as possible. Make a diagram showing the *growing point*, the *young leaves*, the position of attachment of the *older leaves* with axillary buds and the young *vascular bundles*.

The Brussels sprout is a large bud whose outer leaves become mature with very little elongation of the internodes.

(2) More detailed study of the shoot apex can only be made upon prepared sections. Examine a longitudinal section passing through the shoot apex of privet (*Ligustrum vulgare*), and compare it with a transverse section showing the arrangement of the leaf rudiments and young leaves around it. In the longitudinal section note the *meristem*, *dermatogen*, *vacuolating cells*, *desmogen strands*, *leaf primordia* and *axillary primordia*. Make a diagram of the apical tissues and drawings of cells characteristic of the different parts.

(3) A model experiment illustrating the effect of growth pressures upon young cells can be carried out as follows. Make a number of plasticine spheres about a quarter of an inch in diameter, and dust their surfaces with French chalk. Put them into a container such as a small cup or the metal cap of a thermos flask. Choose a glass stopper whose top fits loosely into the container; turn it upside down and press down hard upon the pellets. Remove the stopper and take out the pellets, noting which were in the centre and which near the walls of the container. Count the sides and note their shapes and compare with Fig. 134. Those near the wall of the container will show flattened outer walls similar to those of desmogen cells restrained by their cuticle. Cut the pellets into "halves" with a sharp knife and note the shapes of the resulting sections.

Repeat the experiment, but press only lightly on the plunger. When the pellets are taken out note that they still have rounded corners since the pressure was not enough to eliminate completely the interpelletary spaces.

## Chapter XVII

### THE FOLIAGE LEAF: TRANSPIRATION

The shoot or aerial part of the higher plants is differentiated into two main organs, stem and leaf. The leaf is the organ of photosynthesis and its principal tissue is the mesophyll, which contains the great majority of its chloroplasts.

#### FORM

The essential feature of the normal foliage leaf is a thin sheet of tissue, the lamina, which is freely exposed to air and light. The lamina is commonly attached to the stem by a leaf-stalk, the petiole, which at the point of attachment to the stem may swell out to form a more or less conspicuous leaf base (Fig. 138 B), often with two lateral wings of tissue, the stipules. Most leaves have petioles, but in some they are either very short or entirely absent so that the leaf is sessile, i.e. attached direct to the stem by a narrow base (Fig. 138 C-K). Among monocotyledons the leaf is usually much longer than broad and has no constriction at the base, but is attached to the stem by its entire width (Fig. 138 A and B). Vascular conducting strands pass out from the stem and pursue a more or less parallel course along the strap-shaped leaf until they approach the tip where they run together. Leaves with petioles usually have a prominent midrib running from the petiole to the tip of the leaf which throws off branches to left and right. These branch again many times and the veins become more and more minute, and finally end blindly in the lamina (Fig. 138 H). Leaves with this reticulate type of veining are of the most varied shapes; a few of which with their descriptive names are shown in Fig. 138 C-K.

The shape is not necessarily constant in all parts of the plant; for example, leaves on the upper part are often more dissected than those towards the bottom (Fig. 139); and the submerged leaves of water plants are usually simpler in outline than those that come above



water. Such modifications seem to occur as responses to external conditions such as light and water supply. Others are more drastic and apparently more ingrained. It may even be difficult at first sight

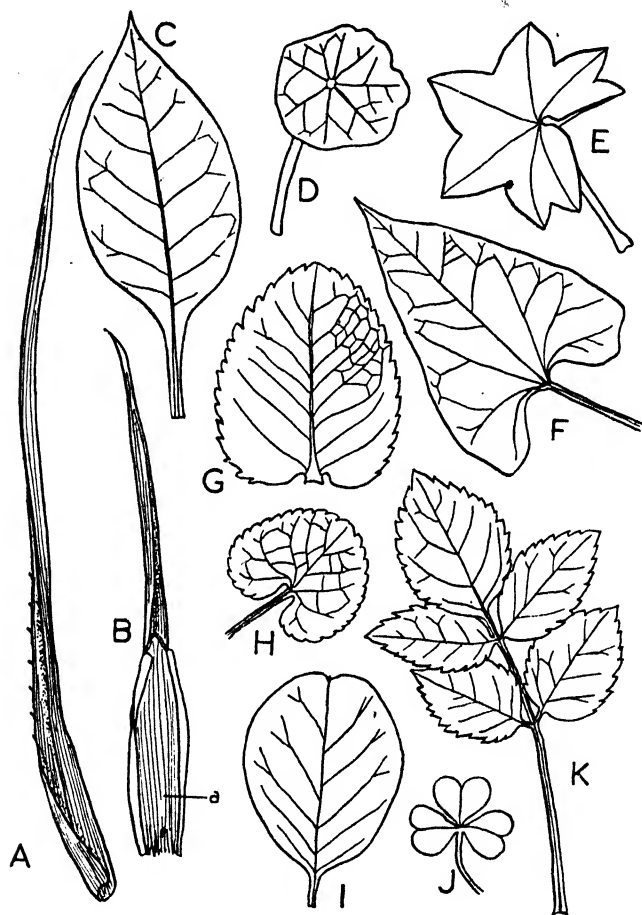


FIG. 138.—Foliage leaves of angiosperms. A and B, leaves of monocotyledons with long, narrow shape, parallel veins and broad base; *a*, leaf-sheath that clasps the stem. The following examples are broad leaves with reticulate venation, petioles and the following shapes: C, belladonna, ovate; D, *Tropæolum*, peltate; E, ivy, palmate; F, wild arum, hastate; G, cordate; H, violet, reniform; I, box, obovate; J, oxalis, trifoliate; K, elder, pinnate.

to recognise their products as leaves at all. The scale leaves of rhizomes and corms (Figs. 107 and 111) and the bulb scales (Fig. 113) described in the last chapter can be recognised by the history of

their development as corresponding with foliage leaves, but have few of their normal characters. The bud scales of woody twigs (Fig. 169, p. 262) come under the same heading. Leaves may also be reduced wholly or partly to tendrils (Fig. 140 B). Another external modification is seen in the spines of *Berberis*, that can only be recognised as equivalent to leaves from the fact that side shoots are produced in their axils (Fig. 140 C and D).

Between the extremes of the wide, spreading lamina and the spine, many modifications are found associated frequently with special habitats. *Succulent* leaves are much thickened by water tissue and

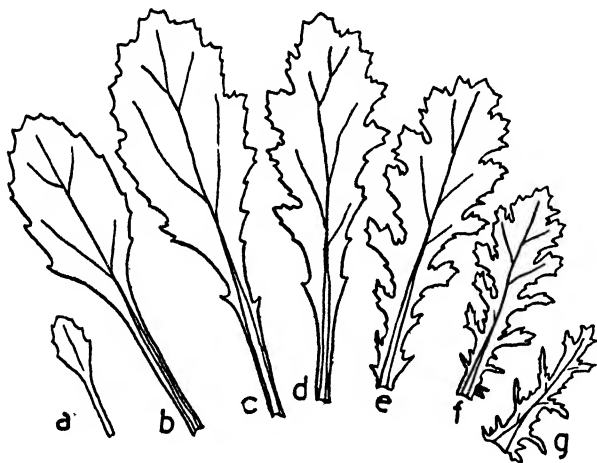


FIG. 139.—Leaves of *Senecio vulgaris* (groundsel). a–g, leaves from successive nodes starting at the base.  $\times 2/3$ .

reduced in surface. They may be oval or even circular instead of flat in cross section (Fig. 140 A). *Xeromorphic*<sup>1</sup> leaves show a variety of characters such as thickening of the cuticle, rolling up of the lamina (Figs. 141 and 142), specially protected grooves in the under-surface, hairiness and needle form. These characters tend to reduce the loss of water from the leaf, but so many other factors enter into the matter that xeromorphic leaf structure may in practice be found associated with quite rapid rates of water loss.

#### STRUCTURE

The lamina of the leaf consists of an upper and lower epidermis and the intervening mesophyll which is penetrated by the veins of vascular tissue.

<sup>1</sup> Greek ξηρος (xeros), dry, and μορφή (morphē), form.

*Mesophyll*

In a typical dorsiventral leaf having distinct upper and lower surfaces, the mesophyll is commonly divided into two layers, the palisade towards the top and the spongy mesophyll below (Fig. 143). The cells of both layers have chloroplasts but they are more abundant in those of the palisade. The spongy cells are more or less isodiametric and have large spaces separating them. This results from the fact that they stop dividing and round off at an earlier stage

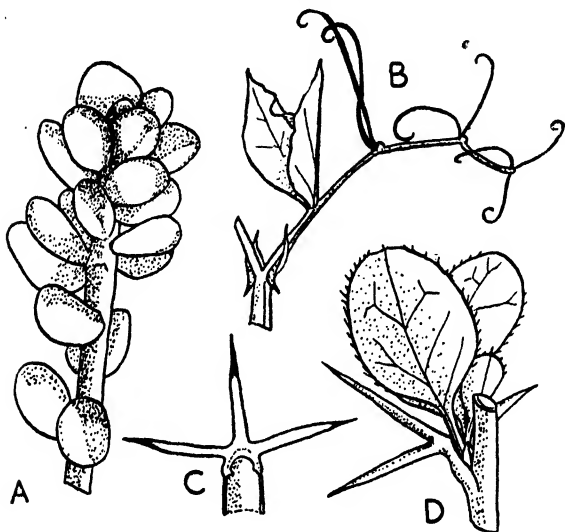


FIG. 140.—Modified leaves. A, succulent leaves of *Sedum adolphii*. B, sweet pea leaf showing one pair of flat leaflets and three pairs as tendrils. C, spines formed by modified leaf of *Berberis*. D, the same showing lateral shoot in its axil. All  $\times 2/3$ .

than the palisade and epidermal cells and so are pulled apart. The palisade cells go on dividing longer in the plane vertical to the leaf surface, but not in the plane parallel to it. As a result they form a more compact tissue of long cells (the palisade) with one, two—most commonly two—or occasionally more layers (Fig. 143 a). Although they are smaller and less noticeable, there are intercellular spaces in the palisade as well as in the mesophyll, and they play a most important part as the paths of gas exchange with the outside air.

*The Veins*

The vascular bundles penetrate the mesophyll, becoming finer and finer as they depart from the midrib and the leaf base. They consist

essentially of xylem, including vessels, tracheids and some parenchyma, above; and of phloem, principally sieve-tubes and companion cells, below. In the large veins these tissues are surrounded by a bundle sheath of mechanical tissue which is sometimes lignified or

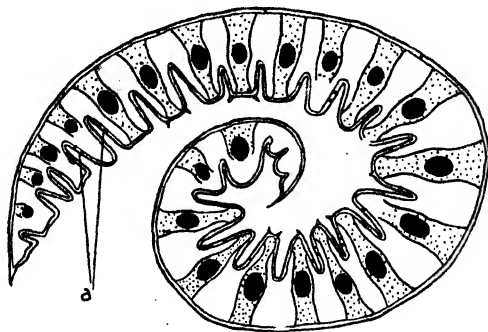


FIG. 141.—Transverse section of the leaf of *Elymus* (lyme grass) which grows on sand dunes; *a*, stomata in the grooves of the upper surface that becomes in-rolled.  $\times$  about 10.

may consist of collenchyma. This sheath is usually most highly developed on the lower side below the phloem, with the result that the veins jut out and are most prominent on the underside of the leaf. The veins thus help to stiffen the leaf lamina, acting rather like

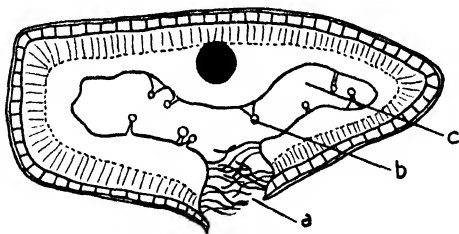


FIG. 142.—Transverse section of *Empetrum* leaf. *a*, hairs; *b*, glandular hairs. The stomata are distributed over the surface of the leaf, opening into the still-air chamber; *c*, palisade shown by light vertical shading. Midrib black.  $\times$  about 10.

the ribs of an umbrella. A thick cuticle and thick walls to the surface cells may also be important in keeping the lamina extended, especially in evergreen leaves of leathery texture. In the finer veins the mechanical tissue gradually dies out and the number of vessels and sieve-tubes becomes progressively less. The bundles (Fig. 143 *d* and *e*) are then usually surrounded by a sheath of a single layer

of parenchyma cells, which may or may not contain chloroplasts. Then the sieve-tubes come to an end, and the bundle is reduced to a row of spiral or annular tracheids. Not every mesophyll cell is in

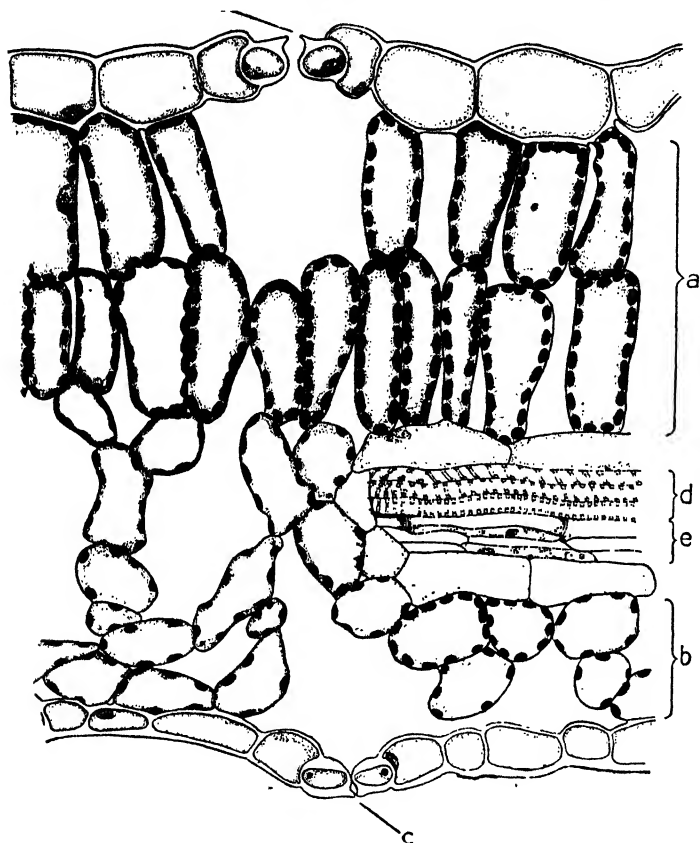


FIG. 143.—Vertical section of a small piece of rhubarb leaf; *a*, palisade; *b*, spongy mesophyll; *c*, stomata, present in this leaf on both upper and lower surfaces. Notice the large intercellular spaces behind them; *d*, xylem; *e*, phloem with sieve-tubes and companion cells. A bundle sheath of living cells without chloroplasts surrounds the bundle and links it with the assimilating cells.  $\times$  about 300.

direct contact with the bundle sheath; but none of them is far away and all are in communication with it through a few other mesophyll cells.

Water coming up from the roots, through the xylem channels that are continuous from the rootlet upwards, passes from the tracheids into mesophyll cells by osmosis. Dissolved salts are also slowly

absorbed and utilised in the formation of organic materials. The sugars and amino-acids formed in photosynthesis diffuse out of the mesophyll cells into the bundle sheath and thence into the sieve-tubes, and so into the midrib and out of the leaf into the stem.

### *Epidermis*

The epidermis consists of tightly joined cells without intercellular spaces whose form has been described on page 199. They continue to

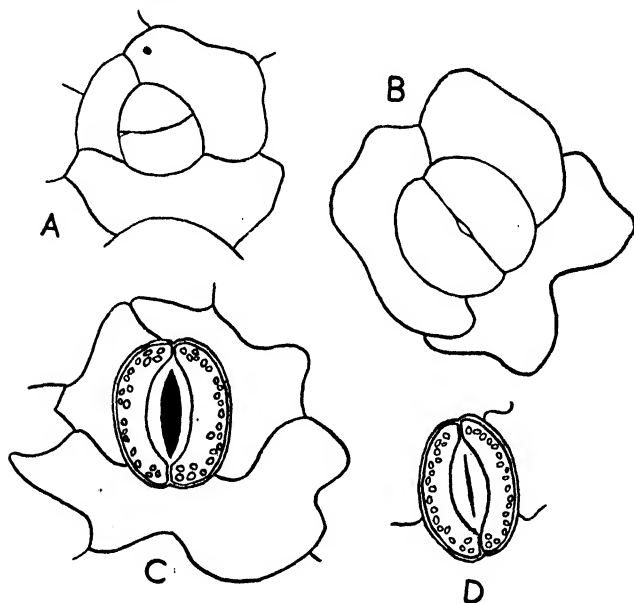


FIG. 144.—Development of a stoma of a belladonna leaf. A, stoma initial showing young guard cells formed by continued divisions after neighbouring cells have ceased to divide. B, guard cells highly turgid and beginning to split apart at the middle of their common wall. C, guard cells still turgid, split complete and chloroplasts formed. D, opening collapsed and closed owing to wilting of the guard cells.  $\times 660$ .

divide, especially in the islands between the main veins, until all other cell divisions have stopped. At the same time they secrete the varnish-like cuticle all over their outer surface and so make an uninterrupted impervious layer over the leaf. The epidermis is usually one cell-layer deep; and upper and lower epidermis are alike except that the upper generally has the thicker cuticle.

*Stomata.*<sup>1</sup> The epidermis is pierced by numerous minute stomatal pores each surrounded by a pair of specially modified cells,

<sup>1</sup> Greek, plural of *στόμα* (stoma), a mouth.

the guard cells. After the general growth of the epidermis is complete, some cells go on dividing for a few extra divisions until a pair of daughter cells is formed that becomes highly turgid and swells out in all directions. It pushes out into the surrounding, less turgid cells, and in surface view forms a circle (Fig. 144). The resistant cuticle which has already formed prevents its cells from swelling upwards so that, in the solid, they are not spherical but bun-shaped. A minute split appears in the middle of the dividing wall (Fig. 144 B), which gradually enlarges as the two cells round off into two separate sausage-shapes, making an open pore (the stomatal pore) between them. The cuticle on the outside and lining the pore is much less elastic than the cellulose of the cell wall. As the cellulose layer con-

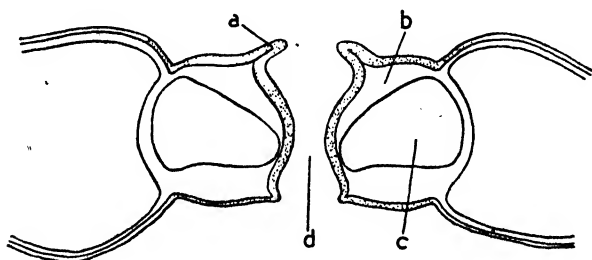


FIG. 145.—Stoma of belladonna leaf in vertical section with pore open. *a*, cuticular fold; *b*, cellulose wall; *c*, vacuole which is surrounded by a protoplasmic lining, not shown; *d*, stomatal pore.  $\times 1500$ .

tracts during the rounding off of the guard cell, the cuticle is consequently thrown up into a fold that gives the stomatal opening a very characteristic shape (Fig. 144 C, and Fig. 145 *a*).

The stomata thus arise with their guard cells in a highly turgid state. They contain numerous chloroplasts and are apparently able to photosynthesise. The sugars they form accumulate in the guard-cell vacuoles, and the resulting osmotic pressure maintains their turgidity. Nevertheless it is observed that the pores of stomata are sometimes closed. This happens when the guard cells lose turgor and sag together. The sugars have not escaped from the guard cells when this happens; but have largely been converted to starch which appears as grains in the chloroplasts. Unlike the starch grains of other green cells, these disappear when the leaf is illuminated, causing the sugar concentration to rise sharply and the turgor to increase correspondingly. The details of stomatal action vary a good deal in different species. Apart from the presence or absence of light, most stomata show a daily rhythm, being open in the mornings and

closing at some time during the afternoon, usually while daylight is still quite bright. They are closed throughout the night, except in some cacti which reverse the usual rhythm. Artificial lighting may tend to prolong the open period; but other external factors, such as temperature and atmospheric humidity, do not have clearly defined effects upon stomatal posture.

*Situation of Stomata.* The stomata of many leaves lie flush with the general level of the epidermis. Different rates of growth of the surrounding epidermal cells may result in the stomata being raised on papillæ or sunk at the bottom of depressions (Fig. 146). Stomata are usually much more abundant in the lower epidermis than in the upper, which may be entirely devoid of them. In many xeromorphic leaves the lower surface is so in-folded in one way or another (Fig. 142), that the stomata open into an enclosure instead of the open air. The tendency of this is to slow down both water loss and photosynthesis by keeping the air immediately outside the stomata comparatively still.

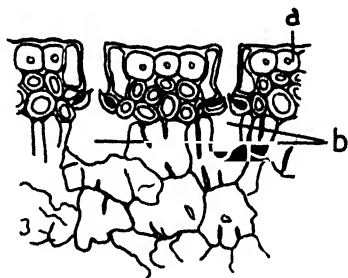


FIG. 146.—Stomata of *Pinus pinaster* leaf. *a*, thick-walled epidermis with stomata sunk in pits; *b*, air cavities inside the stomata, cf. Fig. 143.  $\times 130$ .

#### TRANSPIRATION

The cells of a living leaf need to be saturated with water to remain alive and, except in the wettest of weather, are liable to lose it by evaporation. The external surface of the leaf is not, however, a moist surface from which evaporation goes on freely, but is, on the contrary, a varnished waxy coating through which water penetrates only very slowly. In this the leaves of higher plants differ very much from those of mosses and other simple plants which have no such insulating layer, and do lose water all over their surfaces. This is one reason why many of them can survive only in moist habitats. Among the higher plants themselves, some have very thin cuticles and lose water by direct evaporation also. These are the "shade plants" inhabiting woodlands, where the evaporating power of the air is not severe.

The cells of the mesophyll have no cuticle and water evaporates freely from their wet, cellulose walls into the large intercellular spaces. The air of these spaces thus tends to become saturated, but if the air outside is warm and dry the water vapour diffuses slowly



through the pores of the stomata and is borne away on the wind. A continuous sequence of water loss is set up and goes on so long as the stomata remain open. This is the typical day-time condition. At night the temperature falls and with it the evaporating power of the air; the stomata close and evaporation comes practically to a standstill.

It has been calculated that in many circumstances the loss of water from a leaf is roughly equal to the loss from a free surface of water of the same size and shape. This seems surprising at first sight since the stomatal pores only amount to about a hundredth of the total leaf surface. It is accounted for by two facts. In the first place the actual evaporating surface, the total area of all the mesophyll cells where they abut on intercellular spaces, is many hundreds of times greater than the external surface of the leaf. Secondly, the rate of diffusion of vapours and gases through minute openings has been shown to be fast out of all proportion to their area. It is evident that the leaf is not a perfectly adjusted organ for the conservation of water vapour. It is, however, good enough to have enabled the higher plants to colonise vast areas of the world's land surface, forbidden by their atmospheric dryness to simpler plants.

### *Wilting*

Leaves not only lose water to the atmosphere, they receive it from the stem and, by way of the roots, ultimately from the soil. The amount of water in the leaf cells thus depends on the difference between the rates of loss and gain. During the day the amount of water in the leaf diminishes, but at night, when transpiration is cut down, the leaf cells absorb water by osmosis from the vessels until they become fully turgid again. There is thus a well-marked diurnal rhythm in the amount of water in the leaf with a minimum somewhere in the middle of the day. In soft leaves this may lead to a temporary drooping, i.e. wilting, since the mesophyll cells cease to press against one another and stretch the epidermis taut when they are no longer fully turgid (cf. p. 61). When a leaf has wilted, the guard cells lose water also and so close the stomata. Contrary to a common belief, closure of the stomata does not anticipate wilting, but follows it. It then cuts down further losses of water, and stops photosynthesis at the same time. If wilting is prolonged or frequent, growth is retarded also.

### *Significance of Transpiration*

The leaf being what it is, it is inevitable that transpiration should take place. It represents a potential danger to the plant and the

ability to sustain a certain amount of transpiration is a condition of the higher plant's existence in the sort of habitat it has colonised. There is, however, another side to the story. As is so often true, the features useful to the plant's existence are, as it were, an accidental result of a process brought about by quite unrelated causes. Evaporation cools the leaf which would otherwise heat up owing to the absorption and conversion of light falling upon it. The scorching of leaves in hot and humid greenhouses is probably due to intense lighting combined with slow transpiration. The transpiration stream, which replenishes the water lost by the leaf, may also be an agent in bringing nutrient substances into it. Active transpiration cannot, however, be considered essential to the plant, or at least to all plants, because it has been found that many can be grown satisfactorily in well-nigh saturated air in which transpiration takes place very slowly indeed.

### Practical Work

(1) Make a collection of **mature leaves** from any one of the following species and make sketches of their outline. Compare leaves from the top of the stem with those from the bottom. Musk mallow (*Malva moschata*), ivy (*Hedera helix*), groundsel. Collect dandelion leaves from different habitats. Sketch and compare their outlines.

#### LEAF STRUCTURE

(2) Take a leaf of the large garden shasta daisy (*Chrysanthemum maximum*). Sketch the *outline* and *veining*. Note the difference of the *upper* and *lower surfaces*. The upper looks dark green on account of the close packing of the palisade cells immediately below the epidermis, and the lower looks greyer on account of the air among the spongy mesophyll cells ("frosted glass" effect).

Put the leaf under water in a vacuum jar and exhaust with a filter pump. Note the air escaping through the *stomata*. When bubbling stops, disconnect and allow air to re-enter the jar. It will drive water into the *intercellular spaces* and the leaf at once becomes translucent, since the water has nearly the same refractive index as the cell walls.

(3) Strip the lower epidermis from a patch of the leaf by tearing sharply across the veins. The **spongy mesophyll** will be exposed and its porous texture can be appreciated even with the naked eye. Lay a piece on a microscope slide, exposed side upwards, and focus a strong light through it. Examine with the low power, focusing up and down in the depth of the mesophyll so as to get a three-dimensional view of its spongy texture, made up by the irregularly stellate cells touching at the points and surrounded by air-spaces.

(4) Cut a **vertical section** of a piece of the lamina without large veins. Hold the piece in a split carrot or piece of elder pith while cutting. Mount a section in (a) dilute glycerine, (b) in a drop of alcohol followed by dilute glycerine. Examine under the microscope. The spirit will displace the air from the intercellular spaces owing to its low surface tension, but will decolorise the chloroplasts. If difficulty is experienced in getting a good enough section, use material that has been hardened in alcohol for a week or more.

Note the *epidermal layers* and look for *stomata* in both. Note that the stomata project slightly from the general surface and that their walls are thickened top and bottom. Examine the *palisade* of one or two layers with large cavities below the stomata; the *spongy mesophyll* and small *veins* with *xylem* and *bundle sheaths* with a few chloroplasts. There will be no phloem in the small veins. Draw a portion of the leaf from top to bottom.

(5) Strip away a piece of the lower epidermis, as before. Bend the leaf over the left forefinger and cut away a thin slice of the exposed mesophyll with a sharp razor. Mount in dilute glycerine and draw the *spongy mesophyll* cells and one of the *fine veins* passing through them and consisting of two or three spiral vessels and a parenchymatous bundle sheath only.

(6) Cut a section across the *midrib*. Mount in dilute glycerine. Make a drawing showing *xylem*, *phloem*, *collenchyma* and *epidermis*. Treat sections with aniline chloride and chlor-zinc-iodine to determine the nature of the thickened walls; but do not draw after treatment with chlor-zinc-iodine since it causes the walls to swell rapidly. Note the *cuticle*, especially on the guard cells of the stomata.

(7) Mount a piece of the stripped *lower epidermis* in water. Draw a few of the large *epidermal cells* with wavy walls, large *vacuoles*, sparse *chloroplasts* and large *nuclei*. There are no intercellular spaces. Include a *stoma* in the drawing, showing the two sausage-shaped *guard cells* with numerous *chloroplasts* surrounding the open elliptical *pore*. The stoma is raised slightly above the epidermal cells whose walls can be seen overlapping its edges by focusing slowly downwards. Mount a second piece of epidermis in 50 per cent. glycerine and note the closing of the stomata.

(8) Prepared transverse sections of other leaf types should also be examined, particularly *Iris* or another monocotyledon; a xeromorph, such as *Hakea*, *Festuca*, *Erica* or *Nerium oleander*; a succulent, such as *Rochea falcata* or a *Sedum*; and a submerged aquatic such as *Sagittaria* or *Alisma*.

#### TRANSPIRATION

(9) **Potometer.** Fit a bottle with a new cork and cut a hole with a cork-borer into which the stalk of a leafy cherry laurel shoot can be tightly fitted, with the lower end projecting for an inch or more. The cork should have a second hole or slit down one side to permit the passage of air. Fill the bottle with water and insert the cork with the shoot. Dry carefully and weigh on a strong balance to the nearest gram. Allow to stand for one hour and weigh again. Cut off all the leaves, leave for a further hour and weigh once more. Water will be evaporated from the leafy shoot, but little or none from the bare stem.

(10) **Water Loss via the Stomata.** Take two leaves of equal size having thick cuticles and stomata on the lower surface only. *Ficus elastica* and cherry laurel are suitable. Vaseline the upper surface of one and the lower surface of the other. Tie a string or piece of cotton to the petiole of each; hang on a balance and weigh. Leave exposed to the air for several days and then weigh again. Vaseline the lower surface, thereby blocking the stomata, will be found to have retarded loss of weight due to loss of water.

(11) **Raising of Water by Transpiration.** Fit the cut end of a shoot of cherry laurel with a piece of rubber tubing and a long length of glass tubing filled with water and dipping into a strongly coloured dye solution. Avoid mixing. The water must wet the end of the shoot and no air bubbles must be included. Clamp in an upright position. As water evaporates from the leaves of the shoot, further water will pass in from the tube, as shown by the rise of the dye.

## Chapter XVIII

### THE PRIMARY STEM

The stem forms the branching axis of the shoot, and bears the leaves that are attached directly or by petioles to its flanks. It thus supports and distributes the leaves in the light and air, whence they derive the ingredients of photosynthesis; and it acts as their channel of communication with the roots, whence they derive their further requirements of water and salts. In addition, the stem performs the same offices for the flowers, which are themselves specialised shoots, in which the reproductive cells are formed.

#### *Structure of the Primary Stem*

By a primary stem is meant one that is developed from a primary shoot meristem. We shall take as an example the aerial stem of an upright herbaceous annual, the giant sunflower, *Helianthus annuus*. Its structure depends a good deal upon the fact that it is essentially a leaf-bearing organ developing from the same meristem as the leaves themselves. As described on p. 219, the shoot differentiates from the nodes upwards into the leaf and downwards into the internode below. It can therefore in a sense be regarded as an assembly of leaf-stem units successively developed; and this at least serves to emphasise the closeness of the connection between stem and leaf.

#### *Structure of a Young Internode*

The fully organised stem of *Helianthus annuus* (Fig. 147) is a solid, fairly massive structure whose internal arrangements have to be studied mainly in transverse and longitudinal sections. A transverse section of a young internode shows that its most prominent features are the vascular bundles arranged round the outside of the pith (Fig. 148). Outside the bundles is a peripheral cylinder of tissue consisting of cortex and epidermis.

The microscopic structure of these outside tissues resembles that

of the foliage leaf in a number of ways. The *epidermis* has the same character as the leaf epidermis and consists of tightly fitting cells with a cuticle on their outer surface and stomata identical in structure with leaf stomata, but more sparsely distributed.

The *cortex* has two readily distinguishable layers. The outer consists of cells, relatively small in transverse section, which are found

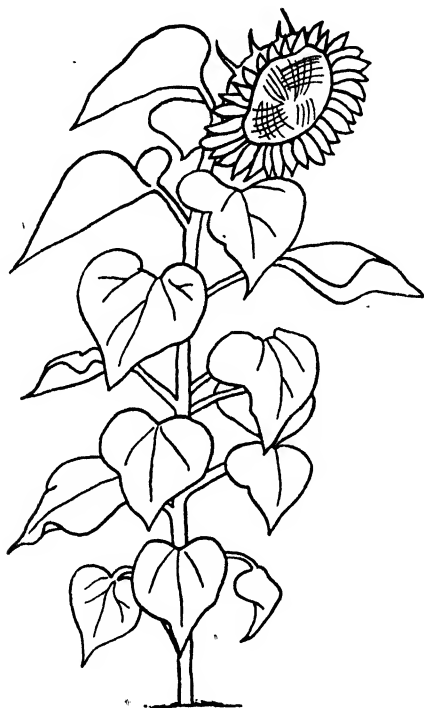


FIG. 147.—*Helianthus annuus*, giant sunflower. An annual plant with a single erect stem. It grows seven to eight feet high.

to be somewhat elongated, in the direction of the stem axis when seen in a longitudinal section. These cells have few intercellular spaces and are collenchymatous, having strips of cellulose thickening running down their corners. In the stems of the giant sunflower the collenchyma is continuous right round the stem (Fig. 148 b) but in softer stems, strips of collenchyma alternate with cells having unthickened walls. Stems with prominent angles, like deadnettles, have their collenchyma at the corners. The softer cells of the outer cortex and some of the larger inner cortical cells have chloroplasts.

They are loosely packed, with rounded corners and intercellular spaces that communicate with one another and with the chambers which form below the stomata. The resemblance of these tissues to a mesophyll is evident, and in plants with reduced leaves they may even form a palisade.

The vascular cylinder is separated from the inner cortex by a continuous *starch sheath*. It is one cell thick and named from the fact that its cells commonly possess starch grains even when the

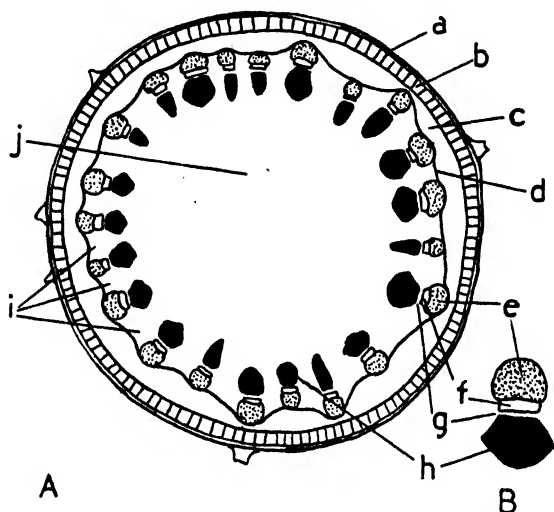


FIG. 148.—*Helianthus annuus*. A, diagram of T.S. young internode of the stem; a, epidermis; b, collenchyma of the outer cortex; c, inner cortex; d, starch sheath; e, pericycle fibres; f, phloem; g, cambium; h, xylem; i, medullary (pith) rays; j, pith. B, vascular bundle, lettering as in A.

neighbouring tissues have none. On treating a section with iodine, the starch sheath is very strikingly revealed. The radial walls of its cells are usually shorter than the tangential and the cells are somewhat elongated longitudinally. They are therefore roughly brick-shaped but with convex, instead of flat, outer and inner faces. The radial walls are tightly fitted together and there are no inter-cellular spaces passing through the starch sheath from the cortex to the tissues inside.

Within the starch sheath the conducting tissues are arranged in a number of *vascular bundles* (Fig. 148 B and Fig. 149). These have differentiated from the desmogen strands and, in most dicotyledonous stems, a thin layer of cells remains undifferentiated and meri-

stematic. This is the cambium (Fig. 149 g), and it is still capable of cell division, unlike the tissues around it. Besides the cambium, each bundle contains a strand of xylem (Fig. 149 h) towards the pith and

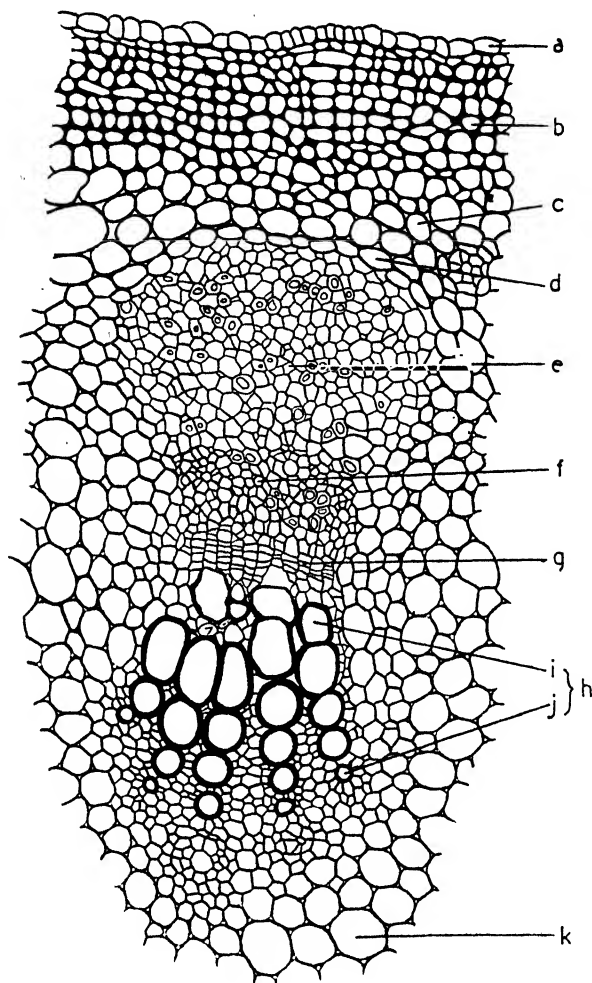


FIG. 149.—*Helianthus annuus*. T.S. vascular bundle and adjoining tissues; a, epidermis; b, collenchyma of outer cortex; c, inner cortex; d, starch sheath; e, pericycle fibres, only a few are heavily thickened; f, phloem; g, cambium; h, xylem; i, metaxylem; j, protoxylem; k, pith.  $\times 100$ .

a strand of phloem (Fig. 149 f) outwards. Separating the phloem from the starch sheath is a capping of fibres (Fig. 149 e), which is part of the pericycle, a layer of tissue part fibrous part parenchymatous.

The bundles of the stem are directly continuous with those of the leaf (cf. p. 219). They are identical in structure with the larger bundles of the petiole and midrib and their orientation is also the same; the outward position of the phloem in the stem corresponds with its underneath position in the leaf.

The stem bundles do not pursue isolated courses from top to bottom of the stem. As already explained, they originate in units divided between leaf and internode. Several bundles supply each leaf and at the bottom of their internodes they link up with the bundles of the one below. The pattern of the linkage depends upon the number of bundles to a leaf, how many leaves are attached at each node, and so on. A comparatively simple example is illustrated in Fig. 150.

In some species the bundles are wide, so that they fuse into a more or less continuous cylinder, as in young rose stems. In *Helianthus* they are narrow with rays of parenchymatous tissue (Fig. 148 i) between. Their phloem consists of sieve-tubes, companion cells and parenchyma. The protophloem, comprising the first narrow sieve-tubes to become differentiated, is on the outside and against the fibres.

In an adult internode the metaphloem has become differentiated right up to the cambium. Similarly, the xylem now consists of the original protoxylem at the tip of the bundle towards the pith (Fig. 149 j and Fig. 124 a and b) and the more slowly differentiated metaxylem continuous up to the cambium, on its inner face (Fig. 149 i). The metaxylem consists of large scalariform, reticulate and pitted vessels (Fig. 124 e-h), together with xylem parenchyma which retains its living contents and divides horizontally instead of elongating, but has its walls lignified in varying degrees. Some stems with an unusually great development of phloem, as in vegetable marrow, have phloem strands on the inside of the bundles as well as outside the xylem. Such bundles are termed bicollateral to distinguish them

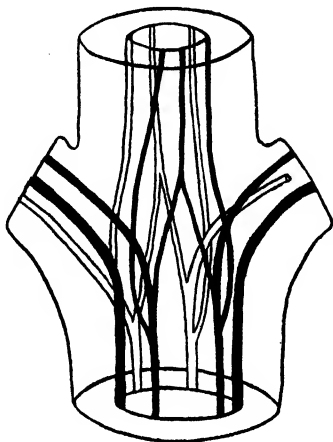


FIG. 150.—Diagram of the linking of the vascular bundles at a *Clematis* node. Three bundles are shown entering from each of the opposite leaves and linking with the six bundles from the node above.



from the more normal collateral kind found in the sunflower.

The centre of the stem is occupied by the medulla, or pith, whose cellular characters have already been described (p. 218).

### *The Monocotyledonous Type*

The leaf and stem structure of monocotyledons is so radically different from that of the dicotyledons so far described, that it must



FIG. 151.—*Zea mays*, maize, plant showing stem with sheathing leaf bases and two inflorescences, staminate above and pistillate below. The stems grow 6–8 feet high.

be sketched at least in outline. Its peculiarities arise from the fact that the leaf primordia of monocotyledons, although they begin as papillæ, rapidly spread laterally until they completely encircle the stem. The leaf initials thus become a succession of concentric sheaths round the stem (Fig. 136 B) and their bases retain this character permanently, even though the blades open out into flat strap-shaped laminæ. The adult structure of the monocotyledonous type of stem is still dominated by the fact that at each junction with a leaf a ring of vascular bundles, stretching almost completely round

the stem, passes outwards into the leaf base and downwards into the internode below. This leads to a sharp contrast with the dicotyledonous type in which a few bundles at one side are collected into a comparatively narrow petiole at each leaf insertion.

*Zea mais* (maize; Fig. 151) produces a large annual stem built in the monocotyledonous fashion, which may be taken as typical. A transverse section of an internode (Fig. 152) shows what appears at first sight to be an irregularly scattered collection of bundles in a

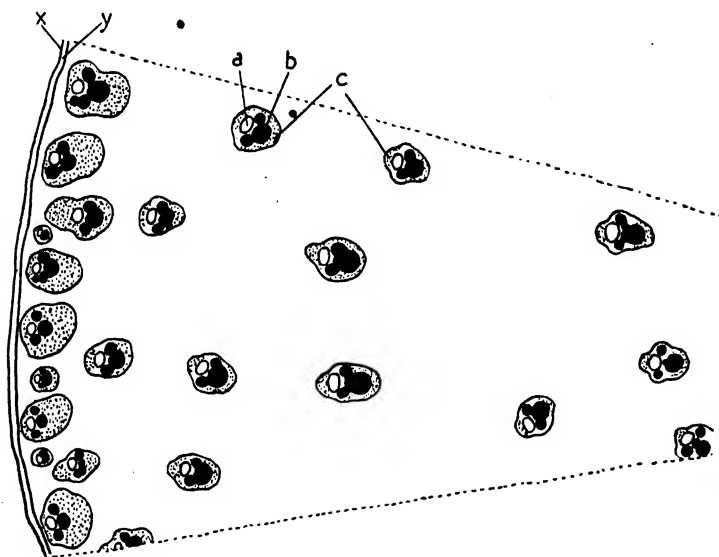


FIG. 152.—*Zea mais*, diagram of T.S. of part of a young internode; showing the vascular bundles scattered in the ground tissue; *a*, phloem; *b*, xylem; *c*, bundle sheath; *x*, epidermis; *y*, fibres.

more or less uniform ground tissue. The bundles are not collected into a single ring, as in *Helianthus* and other dicotyledons, and are, moreover, very numerous, amounting to 200 or more. About half the total number are, however, situated immediately below the surface, and the remainder become more and more sparsely scattered in passing towards the centre. The actual centre of the stem is devoid of bundles and this central parenchymatous zone is much more pronounced in other monocotyledons, such as lily and *Tradescantia*. In many grasses it breaks down so that the stem becomes hollow in the centre except at the nodes, a familiar feature in bamboo canes. It thus resembles the pith of the dicotyledons but

there is no sharp transition from pith to cortex delimited by a starch sheath. The cells of the ground tissue become smaller towards the periphery owing to more frequent divisions, and there is a narrow layer of fibres, one or two cells thick, immediately below the epidermis (Figs. 152 and 155 y). The fibrous layer is interrupted at frequent intervals by groups of cells with unthickened walls occurring where the epidermis is pierced by a stoma. There is a space below the stoma connecting with an inter-cellular space system among the thin-walled cells. In young parts of the stem these have chloroplasts. A photosynthesising layer of this sort is more fully developed in lily stems outside the fibrous layer.

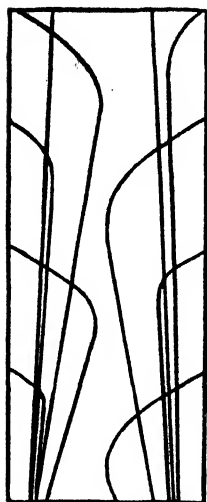


FIG. 153.—Diagram of the courses of some of the vascular bundles in a monocotyledonous stem. Much simplified.

The course of the vascular bundles in the stem can be traced from the node downwards (Fig. 153). Many bundles connect the stem and leaf at the node and pass more or less horizontally to varying depths in the stem. They then turn and pursue a downward course through the internode to the next node where they link up with bundles entering from the leaf below, and again pass on downwards. The anatomy of the nodes is so complicated that it is impossible to say how far down the stem any particular bundle goes before its identity is lost in a final fusion with others. Its downward path is not exactly vertical. Besides minor irregularities and lateral displacements it slowly becomes more peripheral, and this is the reason why in a transverse section bundles are more numerous towards the outside of the stem. It also explains why the vascular arrangements are so difficult to study in longitudinal section.

The structure of the bundles (Fig. 154) is collateral, as in most dicotyledons, that is to say there is a strand of phloem on the outside and of xylem on the inside. The protophloem and protoxylem are on the extreme outside and inside respectively, as before. Elongation of the stem is very rapid and extensive in maize, with the result that the protoxylem is not merely stretched but actually torn apart. In bundles towards the centre of a transverse section, i.e. near their connection with the leaf, the resulting cavity can be seen, often with a ring of the annular thickening lying loosely in it (Fig. 154 a).

Many of the bundles nearer the periphery show no protoxylem, being farther from their connection with their leaf and having differentiated later when extension was complete.

An important feature noticeable in all the bundles is that the metaxylem and metaphloem have differentiated right up to one another and no meristematic, cambial zone is left between, as in the

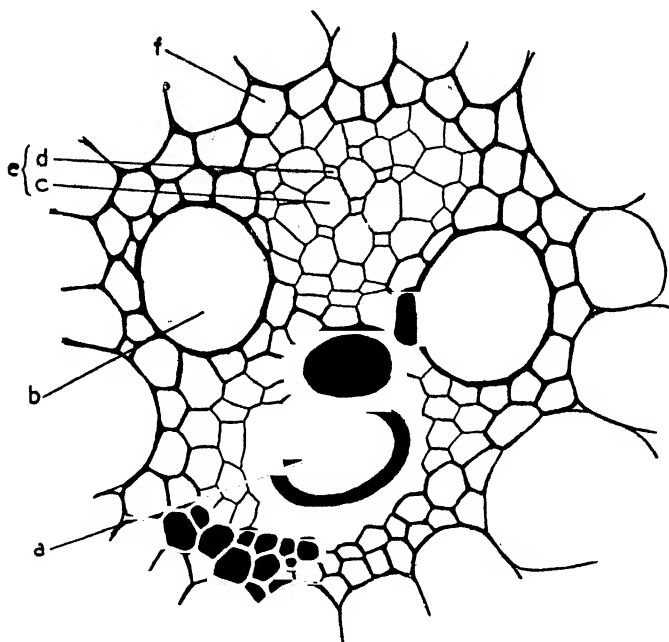


FIG. 154.—*Zea mays*, T.S. deep-seated vascular bundle; *a*, protoxylem, the spiral thickening band has broken loose from the surrounding parenchyma; *b*, metaxylem; *c*, sieve-tube; *d*, companion cell; *e*, phloem; *f*, thin bundle sheath,  $\times 450$ .

dicotyledonous bundles. The development of the bundle is thus finally closed and the bundle is described as a closed bundle in contrast to the open type of the dicotyledons. The metaxylem consists of two large flanking vessels (Fig. 154 *b*) with pitted walls, almost  $60 \mu$  in diameter. One or two narrower tracheids, also with pitted walls, lie between, and there is often a spiral tracheid linking up with the protoxylem. Small-celled parenchyma fills up the sides. The metaphloem is wholly composed of very beautifully arranged sieve-tubes and companion cells (Fig. 154 *d*). Sieve-plates are poorly developed and hard to find even in longitudinal section. There may

be a small strand of unligified parenchyma cells wedged between the metaphloem and metaxylem.

All the bundles are surrounded by a sheath of fibrous tissue. This is thin in the early differentiating parts of the bundles—the central ones of a transverse section (Fig. 154 f)—but becomes much thicker and heavier in the parts differentiating later—the outer bundles of

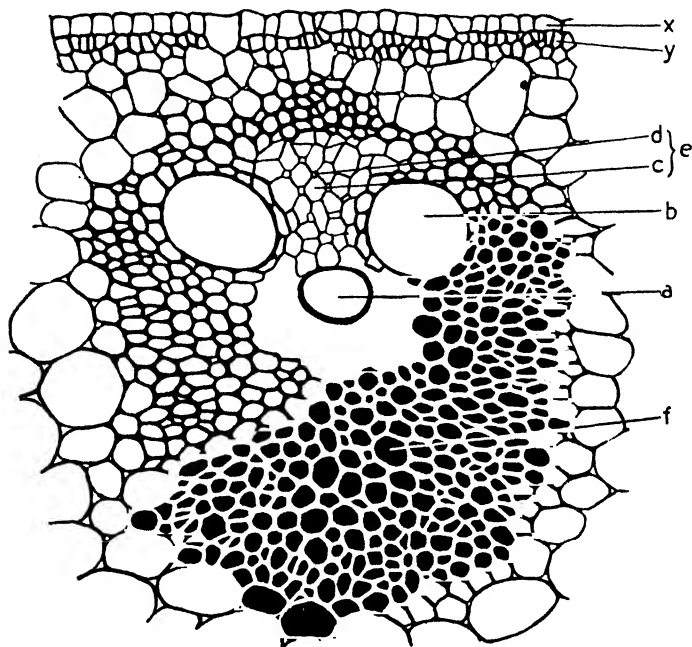


FIG. 155.—*Zea mais*, T.S. outer vascular bundle and adjacent tissues; *a*, protoxylem; *b*, metaxylem; *c*, sieve-tube; *d*, companion cell; *e*, phloem; *f*, thick bundle sheath; *x*, epidermis; *y*, fibres.  $\times 300$ .

the transverse section (Fig. 155 f). Here the thickening is so massive and the bundles so closely placed that it forms an almost continuous fibrous sheath in addition to the sheath immediately below the epidermis (Figs. 152 y and 155 y).

### *Maintenance of the Erect Position*

The uprightness of the very young regions of the shoot is dependent upon the turgor of its vacuolating, internal cells opposed by the comparative firmness of the smaller-celled surface tissues (cf. p. 61). This soon comes to be supplemented first by the development of the collenchyma and later by the development of fibres.

Collenchyma is differentiated at the periphery, just below the epidermis, even while elongation of the internodes is still going on. A complete cylinder of collenchyma is formed in the young internodes of *Helianthus annuus* so that the distribution of the strengthening tissues is the mechanically economical one of a tube, giving maximum strength for the amount of material concerned. Even when the cylinder is broken up into a number of vertical strands, as in other dicotyledons, the arrangement remains strong, because the strands are sufficiently supported by the intervening tissues to prevent displacements. Collenchyma has a very high tensile strength and has been found to sustain a strain of 10–12 kg. per sq. mm. cross-section of wall before breaking. Its elastic limit is much lower, a load of 1.5–2.0 kg. per sq. mm. causing permanent elongation. This capacity for stretching easily without breaking explains how collenchyma is able to afford mechanical support to a young tissue without preventing its elongation.

Fibres which are lignified have a slightly greater tensile strength than collenchyma, but a much higher resistance to stretching before breaking: they are not fully differentiated until stem elongation is complete. Their most typical distribution in the young dicotyledonous stem is as a series of strands in the pericycle, capping the vascular bundles (Fig. 148 e). They are therefore only a little deeper-seated than the collenchyma, which they are in a mechanical sense replacing. They may be thought of as forming a girder system reinforced radially and tangentially by the softer tissues. Both by the properties of their material and by their distribution, they afford a high degree of resistance to lateral displacement or battering down of the shoot, and enable it to maintain the top load of the spreading leaves.

The story is essentially the same in maize, where the heavily fibre-coated bundles are also to be found in the periphery.

### Practical Work

(1) Sketch a piece of the mature shoot of *Helianthus annuus*, marking leaf-blade, petiole, axillary buds, nodes and internodes. Cut through a petiole near its junction with the stem. Examine the cut surface with a lens and make an outline diagram showing the number and position of the vascular bundles.

(2) Stand a young shoot of *Impatiens parviflora* in a 1 per cent. solution of acid fuchsin. When the dye has risen through the stem node and draw the courses of the vascular bundles through the internodes and their junctions at the nodes.

(3) Soak a cross section of a *Helianthus* internode in aniline chloride and then mount in dilute glycerine. Examine under the low power and make an outline

diagram of the distribution of the tissues. Use conventional hatchings to distinguish the xylem, phloem, etc., or colour according to a consistent plan. The following is frequently adopted: *xylem* red, *phloem* blue, *fibres* yellow, *cambium* green. *Epidermis* and *starch sheath* as single black lines. Show the position of each of the above. Mark and label the position of *protoxylem* and *protophloem*; also of *pericycle*, *inner and outer cortex*, *pith* and *rays*, all of which are better left unshaded or untinted.

(4) Make careful high-power drawings of (a) a **vascular bundle**, and (b) small groups of characteristic cells of the **outer tissues**. Label carefully.

(5) Treat with aniline chloride and then examine a **radial longitudinal section** passing through a vascular bundle. Check against your drawings of the transverse section and make drawings of *xylem*, *phloem*, *cambium*, *fibres*, *pith*, *inner cortex*, *collenchyma* and *epidermal* elements. Attempt solid perspective drawings of some of the simpler cells such as fibres and cortical elements. Remember these represent opinions, not facts. Compare your attempts with those of other students.

(6) Examine a **transverse section** of a *Zea mais* **internode** previously soaked in aniline chloride. Make an outline drawing of a quadrant showing the distribution of the vascular bundles. Make a careful high-power drawing of two bundles, one from the centre and one from the periphery. Label the *protoxylem canal*, *metaxylem*, *sieve-tubes* and *companion cells*, *fibres* and *parenchyma* in each.

## Chapter XIX

# THE PRIMARY ROOT ABSORPTION OF WATER AND SALTS

### *The Root System*

Roots are typically colourless axes of the plant which grow downwards into the soil, fixing it in position and absorbing water and salts from the soil solution. When a seed germinates it puts out a radicle that turns downwards, whatever its original inclination, and grows into the main root, descending as vertically as possible into the soil. This *tap root* branches freely, the lateral roots usually growing more or less horizontally outwards from it. The laterals branch again in their turn and so on until a network of fine roots is built up, exploring intimately a surrounding volume of soil roughly the shape of an inverted cone (Fig. 104, p. 181). The development of the system is much affected by soil conditions. Apart from impenetrable layers of rock, root development is much restricted by a close soil texture or actual waterlogging, causing bad aeration; or by excessive dryness. It is, on the other hand, promoted by a good texture providing adequate air and moisture and by rich supplies of nutrient salts. The profusion of the root's branching is much affected by such factors, and reflects the soil conditions in which it finds itself.

Root systems centring upon a tap root are found in the majority of upright annual dicotyledons, but in many plants, such as the plantains, the first root makes little growth and is soon supplemented by a number of adventitious roots arising from the lower nodes of the stem. *Fibrous root* systems of this kind are characteristic of the monocotyledons (Fig. 107 A), but are also found among dicotyledons with runners, rhizomes, bulbs and corms. The underground stems of the latter assist anchorage in much the same way as a tap root.

### *The Growing Point of the Root*

Each root, whether tap, lateral or fibrous grows from an apical meristem, which has much the same structure in all of them. The



meristem proper does not occupy the surface, as in shoots, but is found just behind it. Its cells have typical meristematic characters (cf. p. 48 and Fig. 156 a). They divide frequently and cut off files of cells upwards, from which the root structure is developed.

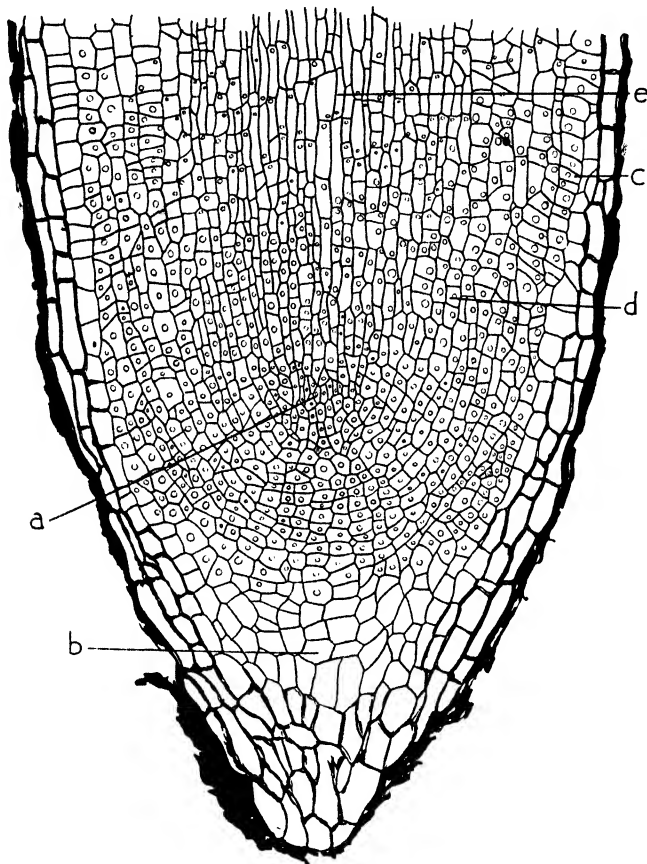


FIG. 156.—Longitudinal section of the tip of a beech root. *a*, meristem; *b*, calyptragen forming the root-cap; *c*, dermatogen; *d*, periblem; *e*, plerome.  $\times$  about 100. From a photograph by Clowes.

In the downward direction some cells are cut off from the lower surface of the meristem to form the root-cap (Fig. 156 *b*). The meristem does not stretch right across the root, but is situated in the centre and there is an evident discontinuity between the flanks of the root-cap and of the young root tissues behind it. This results from the more frequent division of cells formed in the upward

direction and their later vacuolation than those of the root-cap; especially in the layer which comes to the surface (Fig. 156 c).

The cells of the root-cap vacuolate almost at once; their walls become mucilaginous, and they are continually being rubbed away as the root-cap is pushed through the soil interstices. They evidently prevent a similar gradual attrition of the meristem itself, and remains of the cap cells may often be seen adhering to the root surface up to the point where elongation begins.

The root meristem does not produce surface ridges, like the shoot meristem. It has, however, a distinct outermost layer, the dermatogen, which—like that of the shoot—divides only by anticlinal walls. Its outer surface does not produce any cuticle, even when it emerges from the root-cap and is directly exposed to the soil atmosphere. The inner cells also divide principally by anticlinal walls, giving rise to long files of cells which first grow by increasing their protoplasm and then elongate by vacuolation. An outer sheath, the periblem, which gives rise to a wide cortex (Fig. 156 d), may be distinguished from an inner column, the plerome (Fig. 156 e), which gives rise to the procambium from which in turn the conducting strands are formed.

### *The Elongating Zone*

The vacuolation and elongation of the cells above the meristem causes this zone to become longer. As the older zones above are firmly fixed in the soil, this has the result of thrusting the root tip forward into whatever cavity may be available. The elongating zone is detectable externally by its bare surface without either cap or hairs. It is pale and translucent when held up to the light, owing to its lack of differentiated tissues. Inside the root, dark streaks can often be seen with a hand lens, or even by the naked eye, indicating the presence of long intercellular spaces containing air. The cell vacuoles contain abundant sugars in solution with the result that much water is taken up osmotically, causing the thin elastic cellulose walls to be stretched. Some of the cells on the outside of the procambial strand differentiate while still elongating by forming spiral and annular thickenings. They are the elements of the protoxylem.

### *Root-hair Formation*

When elongation is more or less complete, the surface layer begins to form root hairs. During the period of elongation some cells, often

in vertical rows, go on dividing and producing abundant contents with smaller vacuoles than their faster-elongating neighbours. The external surface of these cells is covered outside the cellulose wall with a layer of calcium pectate, more resistant to stretching than cellulose or the pectic materials on the walls of the long cells. The pressure of the cell contents pushes out a papilla where the calcium pectate layer is weakest. The cellulose layer stretches and new cellulose is added at the tip, but formation of new calcium pectate is slower. The wall therefore remains most stretchable at the tip of the papilla and the root hair is pushed out as a long narrow tube (Fig. 157) with sides hardened by a calcium pectate layer similar to that on the cell. In acute calcium starvation root hairs develop abnormally, often throwing out irregular protuberances instead of a regular

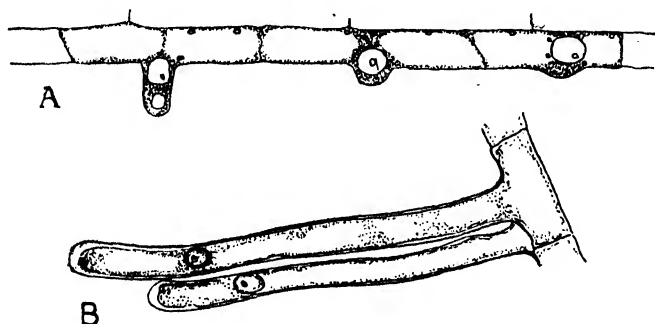


FIG. 157.—A, three cells of the piliferous layer at the beginning of the root-hair region showing early stages of root-hair development. B, fully formed root hairs of *Datura metel*.  $\times 300$ .

tube. The outer pectic layers of root hairs glue themselves into such intimate contact with soil particles that they cannot be detached; but the hairs evidently penetrate and take up the shape of any interstices available in the soil. The simple tubular shape is only realised when plenty of space is available, as in a moist air chamber.

### *Structure of the Primary Root*

A cross-section taken in the upper part of the root-hair region gives the best idea of the root's construction (Fig. 158). In this position the tissues derived from the primary meristem have all differentiated into their various adult forms and later amendments of the structure, as found in old roots, have not yet become important. *Ranunculus repens* roots are convenient for examination as they do not have these complications.

The surface (Fig. 159 a) is formed by the piliferous layer, which has no cuticle but an outer coating of pectic materials. Some of its cells swell out into root hairs. Immediately inside the piliferous layer is a

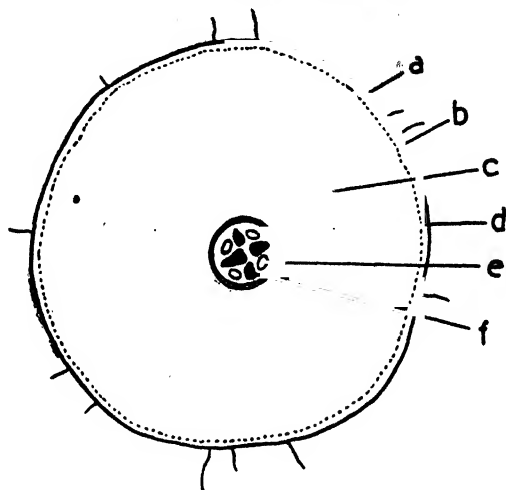


FIG. 158.—*Ranunculus repens*, diagram of T.S. root at the top of the root-hair zone. *a*, piliferous layer; *b*, hypodermis; *c*, cortex; *d*, endodermis; *e*, phloem; *f*, xylem.

second layer of rather similar cells, also small and without intercellular spaces, because the relatively resistant material of their middle lamellæ has withstood the usual rounding-off tendency at the

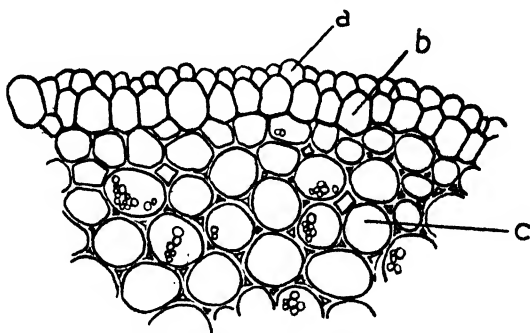


FIG. 159.—*Ranunculus repens*, T.S. part of outer tissues. *a*, piliferous layer; *b*, hypodermis; *c*, cortex.  $\times 130$ .

corners. They appear to contain both pectic and fatty materials that have hardened. Inside this layer, called the hypodermis (Fig. 159 b), is a wide cortex that occupies most of the cross-section of the root (Fig. 158). It is much wider than the corresponding tissue of the

stem. Its cells are relatively large, 50–100  $\mu$  diameter, and have rounded-off corners (Fig. 159 c). They are elongated in the longitudinal direction so their shape approximates to cylinders more than to spheres, and the inter-cellular spaces are also long, continuous and fairly straight. The cortex is consequently very pervious to air, especially up and down the root. The cortical cells have abundant

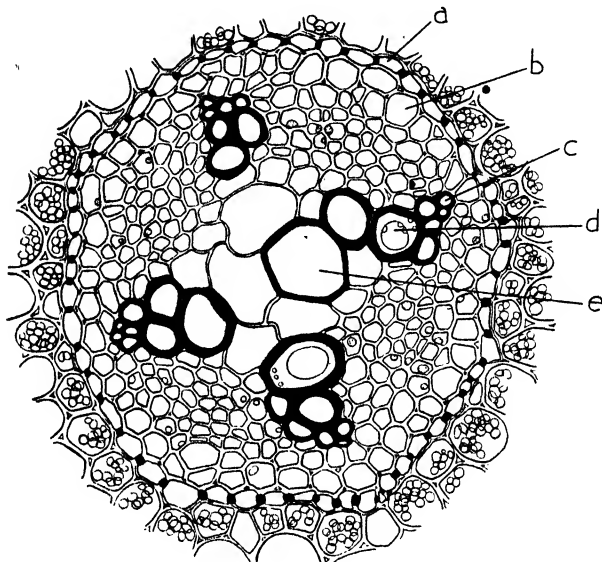


FIG. 160.—*Ranunculus repens*, stele of root. *a*, endodermis; *b*, pericycle; *c*, protoxylem; *d*, intermediate vessel; *e*, metaxylem. Some of the metaxylem is not lignified.  $\times 300$ .

starch grains. The cortex is bounded internally by an endodermis<sup>1</sup> resembling the starch sheath of the stem. Its cells are of the same modified brick shape, and adhere tightly together in a cylinder with no intercellular spaces. Their top, bottom and radial walls are traversed by a specialised strip which is suberised and lignified (Fig. 160 a), called the Casparian strip after its discoverer.<sup>2</sup> The strip occupies the full thickness of the adjoining walls including apparently the middle lamella. It draws up into folds when the endodermal cells are sectioned, but is perfectly flat when the cells are alive. When endodermal cells are plasmolysed or treated with alcohol the proto-

<sup>1</sup> Greek *ενδον* (endon), within; *δέρμα* (derma), skin, i.e. the inner skin, here the skin of the vascular cylinder.

<sup>2</sup> Caspary, 1860.

plasm shrinks away from the other parts of the wall, but continues to adhere to the Casparian strips, giving a very characteristic plasmolysis figure. Since the suberised Casparian strip is impervious to water, there can be no filtration of water or salt solutions from the cortex to the vascular cylinder, or vice-versa, except through the protoplasmic membranes of the endodermal cells. This curious fact obviously has its importance; but its full significance for the economy of the root is still a matter of doubt.

On the inner face of the endodermis lies the pericycle (Fig. 160 b); here only one cell-layer thick, but important because it is in this layer that the initials of lateral roots arise, just opposite the protoxylem elements (Fig. 161).

Below the pericycle and abutting directly on it come the vascular tissues in alternating strands of xylem and phloem. These strands are separated from one another by parenchyma continuous with that of the pericycle. There are several—three to five—protoxylem units (Fig. 160 c) consisting of spiral tracheids of about  $12\ \mu$  diameter in contact with the pericycle. The centre of the root is occupied by a large pitted vessel,  $75\ \mu$  in diameter, and between this and the protoxylems are a number of intermediate vessels and tracheids (Fig. 160 d). The phloem strands are rather less easily observed and lie between the arms of the xylem. Each strand has one or two sieve-tubes and their companion cells.

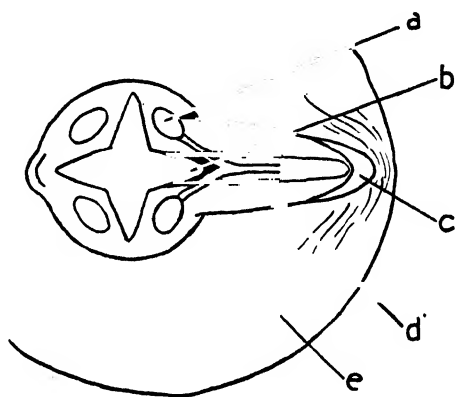


FIG. 161.—Diagram of the origin of a lateral root. *a*, phloem; *b*, protoxylem; *c*, root-cap; *d*, protoxylem of new root; *e*, cortex.

### *Origin of Lateral Roots*

As the zone of the root hairs ages, its root hairs usually wither and die away. Some time later, and correspondingly farther from the root apex on account of the apical growth still going on, lateral roots make their appearance. As seen from the outside, they arise in vertical rows and emerge from small splits which they make in the

outer tissues of the parent roots. They must take their origin from a deeper-seated tissue and in section this is seen to be the pericycle (Fig. 161). Each new rudiment begins to form opposite a protoxylem point, and this is why the lateral roots make their appearance in vertical rows.

A patch of cells divides by tangential walls so that the pericycle layer is doubled. Further divisions occur, building up a cone-shaped meristem and root-cap that pushes out into the cortex (Fig. 161). The endodermal cells also divide to keep pace with the new growth

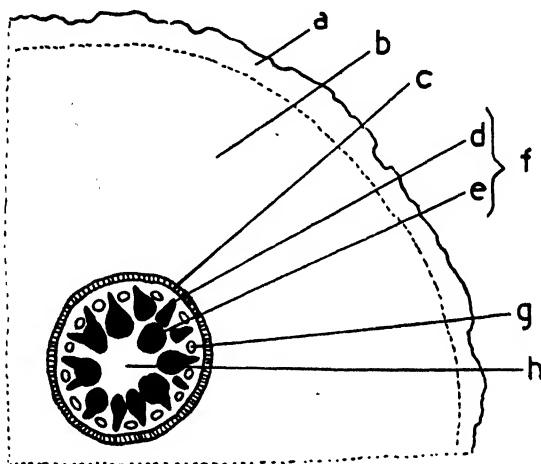


FIG. 162.—*Iris*, diagram of part of T.S. of young root. *a*, hypodermis with remains of piliferous layer on the outside; *b*, cortex; *c*, endodermis; *d*, protoxylem; *e*, metaxylem; *f*, xylem; *g*, phloem; *h*, pith.

and form a sheath over the new initial. The pressure of the growth breaks a way through the cortex, and it is possible that enzymes are secreted from the endodermis, which appears glandular, to assist. While the young root tip is still embedded in the old cortex, xylem and phloem strands begin to differentiate in the usual positions and link up with the corresponding members in the parent root (Fig. 161 d).

#### *Primary Root Structure of Monocotyledons*

The root structure of a monocotyledon such as *Iris* (Figs. 162 and 163) is similar in many respects to that described above. The stele has more numerous protoxylems, with a corresponding number of alternating phloem strands. This condition is described as polyarch. In dicotyledons the number of protoxylems rarely exceeds seven

(heptarch) and may be as few as two (diarch), as in wallflower roots. The metaxylem of the *Iris* root does not reach to the centre, which is occupied by a pith whose cells are more or less isodiametric, but have lignified walls and few or no intercellular spaces. The endodermal cells have heavy U-shaped thickenings on the inner and radial walls, the outer wall in contact with the cortex remaining thin.

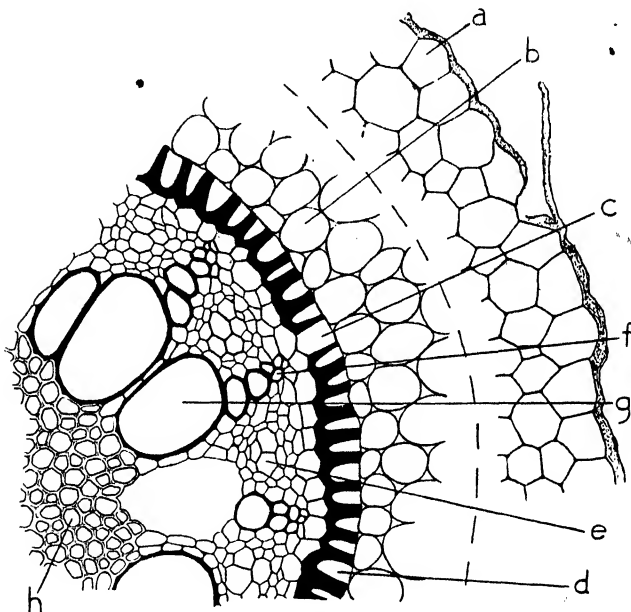


FIG. 163.—*Iris*, T.S. of part of young root. *a*, hypodermis with remains of piliferous layer on the outside; *b*, cortex, the greater part omitted; *c*, passage cell through the endodermis; *d*, endodermal cell with horseshoe thickening; *e*, phloem; *f*, protoxylem; *g*, metaxylem; *h*, lignified pith.  $\times 300$ .

Occasional cells do not have the heavy thickening. They are found opposite protoxylems and are called passage cells (Fig. 163 *c*). Of these features only the polyarch arrangement of the xylem is fairly general among monocotyledons. Some, like wheat, have a large central vessel instead of a lignified pith, and many have an unthickened endodermis.

#### ABSORPTION OF WATER

Water enters a plant from damp soil primarily because it is being lost by transpiration from the leaves. As a result of the loss, the plant becomes unsaturated and able to absorb from sources of



moisture. The structure of the root system, with its widely spreading branches and its multitudinous root hairs, ensures very extensive and intimate contact between the water-deficient plant and the moist soil. The root thus provides a path of entry for the water into the plant; but it is not the active agent, i.e. it does not provide the energy that causes the water to move; this is the latent heat of vaporisation of water, taken up from the air in transpiration. The water deficit is first experienced in the leaves themselves and thence transmitted into other parts of the plant. The transmission depends upon the unexpected fact that water confined in narrow tubes, such as tracheids and vessels, exhibits a very high tensile strength, equivalent to 300 atmospheres or more. As a result, water is actually dragged up into the transpiring leaves, and a water deficit is created in the roots in their turn.

In entering the xylem strands of the roots, water has to pass through the protoplasmic membranes at least at the endodermis (cf. p. 251). This is equivalent to an ultrafiltration through membranes with very fine pores, and much resistance is encountered if the rate of water movement is at all appreciable. If a plant is grown in water and its entire root system is suddenly chopped off below water level, it absorbs water more rapidly through the cut end of the stem than through the entire root system. This apparent paradox would not happen in a moist soil, where the surface of contact provided by the root is all important.

A plant that has wilted on account of rapid transpiration recovers slowly when transpiration is slowed down or stopped. The cells of the leaf mesophyll and other parenchymatous tissues refill themselves with water and again become turgid. This is due to the osmotic properties of their cells (p. 58), and applies to root hairs and other living cells in the root also. The effect of the suction pressure of any cell is to draw water into the cell, and resist its removal from the cell. If cells in contact with one another have different suction pressures, water will pass from one to another until the suction pressures are equalised. Slow adjustments of the water content of parenchymatous tissues may be achieved in this way. Provided one cell of the group, a root hair, for example, is in contact with free water, the whole group will eventually saturate itself.

The refilling of the whole plant with water after transpiration has ceased may be partly due to this effect; but since it can be shown that under such conditions water is actually forced up the non-living xylem vessels, there is evidently some more obscure mechanism

also at work. This is called root pressure, but its origins are still uncertain.

When transpiration is active, the water in the vessels is not under

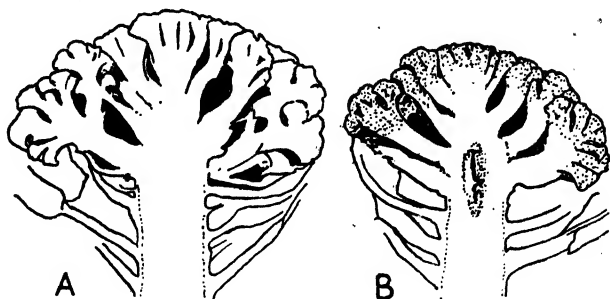


FIG. 164.—Vertical sections of cauliflower heads. A, normal. B, deficient in boron, showing poor development, browning and breakdown of the pith.

pressure, but under tension (Exp. (10), p. 259). Under these conditions the parenchyma cells of the root or leaf do no more than record and transmit the tension. They are in the position of coaches in the middle of a train, which do not themselves pull the guard's van but transmit the pull of the engine to it.

#### UPTAKE OF NUTRIENT SALTS

Although the salts absorbed from the soil are dissolved in the soil solution, the uptake of water and salts are two independent processes going on at quite different rates. The protoplasmic membranes are frequently described as semi-

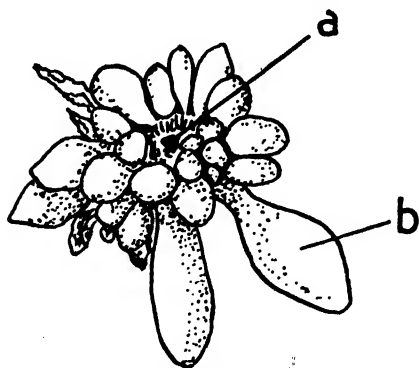


FIG. 165.—*Ranunculus ficaria*, cluster of root tubers lying dormant in the ground during the summer. *a*, scar of aerial shoot that died down in spring; *b*, a root tuber.  $\times 3/2$ .

permeable (see p. 58); and are effectively semipermeable towards salt solutions over short periods of time, such as an hour or so, during which much water may be taken in. The membranes fall short of strict semipermeability when longer periods are allowed, and the entry of salts eventually becomes appreciable.

In a very dilute solution, such as occurs in most soils, salts are fully dissociated and present as ions hydrated by jackets of accompanying water molecules. These may penetrate into surface cells by means of their own spontaneous movements, i.e. by diffusion. This kind of entry is very slow. It has been found that actively growing root tips accumulate salts from dilute external solutions and may build up concentrations in the vacuoles of their cells greatly in

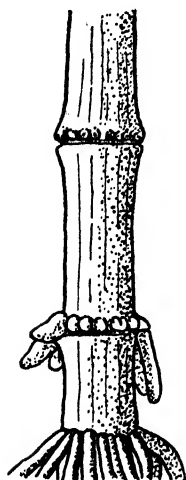


FIG. 166.—*Zea mays*, base of stem showing clusters of thick prop roots, developing from successive nodes.  $\times 3/4$ . After Troll.

excess of those outside. It is therefore clear that the cells take an active part in salt uptake, and are not solely dependent upon salts penetrating their membranes by diffusion and cognate processes. The salt uptake is directly related to the activity of the absorbing cells as measured, for example, by their aerobic respiration. If this is brought to a standstill by removal of oxygen or the use of cyanide, salt uptake is stopped also. The way in which the aerobic metabolism of the absorbing cells is connected with salt uptake and able to promote it, is still uncertain. Old cells in older parts of the root or other regions of the plant are unable to carry on active salt uptake, but the apical region of the shoot probably absorbs salts actively from the neighbouring cells and tracheal sap.

#### *Nutrient Elements Obtained from the Soil*

These are rather numerous and some of the most important are the following: *Nitrogen* is obtained in the form of nitrate or ammonium ions, and is utilised in the formation of protein and other nitrogenous organic compounds. *Phosphorus* is absorbed as the orthophosphate ion,  $\text{—H}_2\text{PO}_4$ , which is an important cellular catalyst (see p. 89). *Sulphur* is absorbed as sulphate ions, and is required in the formation of some proteins and oxidising enzymes depending on the thiol,  $\text{—SH}$ , group. The metals, *calcium*, *magnesium* and *potassium*, are also essential; they appear to regulate the structure and semipermeability of the protoplasmic membranes; they are present as osmotically active substances in the vacuoles and have many other obscure functions. Magnesium is an important constituent of the chlorophyll molecule and iron catalyses the formation of chlorophyll. Besides the above, some “micro-nutrients” absorbed

from the soil have been found recently to be essential to the plant, at least in traces. Examples are boron, necessary for the proper growth of leguminous root nodules (p. 355) and copper, needed for enzymes of the ascorbic oxidase type (p. 89). Molybdenum, manganese and others are also needed, at least by some plants, and are obtained in traces from the soil through the surfaces of the root tips and hairs.

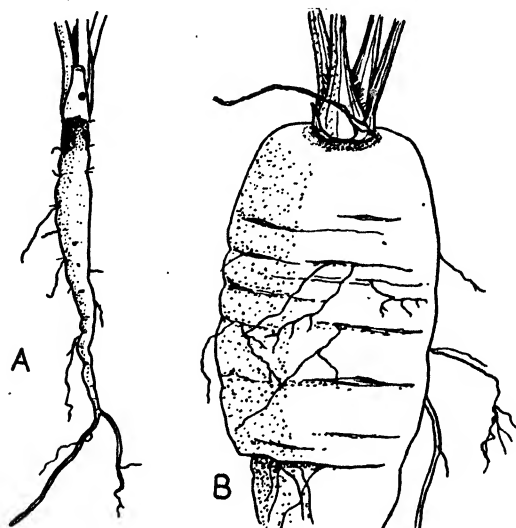


FIG. 167.—Development of the tuberous tap root of *Daucus carota*. A, seedling showing short hypocotyl and stem (heavily shaded) bearing a cluster of leaves. The tap root has begun to swell; the lateral roots remain fibrous. B, mature stage with leaves borne in the hollowed crown (condensed stem). Side roots still fibrous. About nat. size.

### Deficiency Signs

Lack of the essential elements produces physiological diseases in plants, that can be recognised by their external appearance. Lack of nitrogen, for example, causes stunting, pale colour, drying up and excessive woodiness; lack of potassium causes the older leaves to wither and die prematurely while the tip of the shoot goes on growing. These effects may often be seen in plants, especially in cultivated ones, growing on poor soils. Others, such as chlorosis, i.e. complete lack of green pigments, due to the absence of iron, are best studied in water cultures (Exp. (11), p. 259). Starvation effects of the micro-nutrients are often very striking, like the yellowing and internal breakdown of cauliflowers due to boron deficiency

(Fig. 164). They sometimes require very specialised methods of salt purification and water culture to reveal them.

### MODIFIED ROOTS

Some roots become swollen with storage parenchyma in a way reminiscent of the thickened rhizomes and shoot tubers described in Chapter XIV. Adventitious roots form bunches of root tubers in *Dahlia* plants, lesser celandine (*Ranunculus ficaria*) (Fig. 165) and orchids. Thickened adventitious roots from the lower nodes of maize (Fig. 166) form additional supports.

More important are the swollen tap roots produced by carrots (Fig. 167) and parsnips. These begin to form at an early stage of growth below a very much shortened stem and hypocotyl. The stem internodes do not elongate, so the leaves are inserted on a compact crown at ground level. The secondary growth of the additional storage tissues, mainly parenchyma, starts almost at once and continues steadily as the root grows longer, so that the oldest parts are the most swollen and the tap root as a whole has the shape of a long cone. From its flanks come off fibrous side roots, and below the swollen cone the main root is prolonged as a fine thread penetrating vertically into the soil.

This development is completed during the first year of growth and the leaves die off at the approach of winter. In the following season new leaves appear and a flowering stalk is thrown up, the reserves of the root being utilised for its extensive growth. After flowering and setting fruit the plant has completed its biennial cycle and dies.

### Practical Work

(1) **Young Root Systems.** Make a labelled drawing of a mustard seedling that has been germinated in moist air. Note the *root hairs* and the bare *elongating region* between the hairs and the tip. Distinguish the *root* and the *hypocotyl*. Compare with seedlings grown in moist sandy soil and observe the connection between root hairs and soil particles.

(2) Transfer a seedling to a slide. Cover the root tip with water and a coverslip. Do not press the coverslip down. Note the *root hairs*, each arising from a surface cell; and the *meristem*, covered by the *root-cap*. Focus on a surface cell of the elongating region and note its shape and contents. Pass as strong a light as possible through the root and focus downwards into it. The *vascular system* will be seen through the semi-transparent cortex. Dark longitudinal strands indicate the presence of air in *intercellular spaces* of the cortex.

(3) Make a similar examination of the *root system* of a young wheat or barley seedling.

(4) **Lateral Roots.** Examine the surface of a broad bean root three or four inches long. Note the vertical rows (usually four) of lateral roots and the splits

from which they emerge. Twist the upper portion of the root until the cortex breaks away from the vascular cylinder and pull it off. Note the vascular strands of the lateral roots still attached to the central cylinder, showing their internal origin.

(5) **Primary Structure.** Make an outline diagram (cf. Exp. (3), p. 243) of a transverse section of a root of *Ranunculus repens*. Use a freshly cut section treated with aniline chloride or, failing that, a double-stained prepared section. Show the *piliferous layer* (single line), *exodermis*, *cortex* (unshaded), *endodermis* (single line), *pericycle* (label only), *xylem* (line, or red shaded), and mark the *protoxylems* with a cross. Show the *phloem strands* (pale shading or blue). Label all parts carefully. Make high-power drawings of characteristic groups of cells from each of the above tissues.

(6) Examine a **longitudinal section** of the same region and identify as many of the cell types as possible by comparison with the transverse section. Attempt to visualise the shapes of the different cells in the solid.

(7) Make a similar examination of an *Iris* root.

(8) **Root Apex.** Examine prepared longitudinal sections through the apex and elongating zones of maize and bean roots. Make outline drawings indicating the limits of the *root-cap*, *meristem*, *dermatogen*, *periblem*, *plerome*, young *cortex* and *procambial strand*.

#### ABSORPTION OF WATER

(9) Cut off the root of a young bean seedling that has been raised in moist sand. Measure its length. Then immerse it in M/2 calcium chloride solution until it becomes limp and flaccid. Measure again without stretching and then transfer to water. It will become straight and turgid again. When this happens measure its length once more. How do the three measurements compare? What is the explanation of your results?

(10) Take a pot plant of *Pelargonium* that has not been watered for a few days. Cut off the top about an inch above soil level with a razor flooded with water and attach a rubber connection. The rubber must fit tightly, but should not crush the stump, and must at once be filled with water. Push a glass tube about a foot high into the rubber, clamp vertically and mark the water level. Keep under observation and note that the water level drops. When it becomes steady, mark the level and water the pot freely so that the soil becomes wet but not waterlogged. Observe an hour or so later and again next morning when the level will have risen. The initial fall is due to the tension in the water columns of the root when it was cut drawing water into the root system. The leaves having been removed and the soil saturated, the tension is replaced by a positive root pressure. Note that the natural condition was one of tension.

#### NUTRIENT SALTS

(11) Examine the demonstration series of **water cultures** showing the effects of absence of *nitrogen*, *phosphorus*, *potassium*, *calcium* and *iron*. (The management of water cultures, too lengthy to be detailed here, is described in a very practical way in Clarke's *Botany as an Experimental Science*, Oxford, 1935.)

(12) The accumulation of an essential nutrient element, **potassium**, in root tips can be examined as follows. Take a healthy young root tip, preferably one raised in a complete water culture with good opportunities for absorption, and lay it on a microscope slide. Cover with a drop of sodium cobaltinitrite solution (p. 375). The potassium precipitate will be formed abundantly in the cytoplasm of the meristem and in the vacuoles of the elongating cells; but there will be little or none in the root-cap. Any convenient species may be used. Seedling roots raised in moist sand or sawdust will also do; but in them the meristematic and elongating cells will have absorbed the potassium from the older tissues and from the seed—not from outside.

# WOODY PLANTS : TRANSLOCATION

### *Forms of Trees and Shrubs*

Perennial plants of the exposed sort (p. 179) go on growing in yearly cycles, building up larger and larger bodies each season. In the simplest monopodial types the main axis goes on growing vertically, and successive lateral buds form side branches, longest near the ground because they have been the longest growing. The final form is therefore pyramidal, as in the silver birch (*Betula alba*) shown in Fig. 168. The very regular cones of ornamental gymnosperms, the cypresses, Wellingtonias and some junipers, are built on the same plan. Trees like sycamore (*Acer pseudoplatanus*) and horse-chestnut (*Aesculus hippocastanus*) also have monopodial growth but the laterals develop more strongly so that the top becomes wider and more spreading. Usually the lower laterals die away, leaving a bare trunk supporting a crown or "bunchy top."

The growth of a horse-chestnut branch continues in monopodial fashion except when it flowers. The inflorescence bud forms on the shoot apex, and when it has flowered it dies and its remains drop off. Growth is then carried on by one or more lateral buds (Fig. 169 B). Some trees, such as elm (*Ulmus* spp.) and lime (*Tilia* spp., Fig. 170), exhibit such sympodial growth continuously. Towards the end of each season's growth the apical bud dries up and dies and in the following season growth is carried on by the nearest lateral. The cause of the habitual suppression of the terminal bud is unknown, nor does it have any very striking results upon the form of the tree, since the lateral which takes over continues the growth in the original line.

A more drastic result is produced by a failure of the woody shoots to maintain their growth for more than a few seasons. The growth of an elder (*Sambucus nigra*) shoot is extremely vigorous for a few

years ; then it slows down and lateral or adventitious buds from near ground level become active, and throw up new shoots that pass through a similar cycle. In this way a bush is produced instead of a tree. Such shoots may even be produced from roots, as commonly happens, for example, in cultivated roses ; and are then known as suckers, because the vigour of their growth diverts the root sap from the older shoots and may even bring about their death.

Trees and shrubs may be evergreen or deciduous. The leaves of evergreens last for more than a single season and as new leaves are produced meanwhile, especially in the following spring, an evergreen tree like holly (*Ilex aquifolium*) or shrub like laurel (*Laurus nobilis*) is never without leaves. Nearly all the gymnosperms come into this category. In climates such as ours, with more or less severe winters, most broad-leaved (angiosperm) trees and shrubs are deciduous and shed their leaves during the unfavourable season. Larch (*Larix europaea*) is the only deciduous gymnosperm common in this country.

Most of the external features of woody plants can be conveniently studied with twigs in their winter condition. Horse-chestnut twigs are large and of simple monopodial construction except when flowering. The terminal bud is large (the largest of its kind), and consists externally of overlapping bracts of simple shape covered by a sticky resin (Fig. 169 Aa). The bracts are modified leaves formed at the end of the previous season, composed largely of corky cells and gland cells secreting the resin. They form an impervious layer without

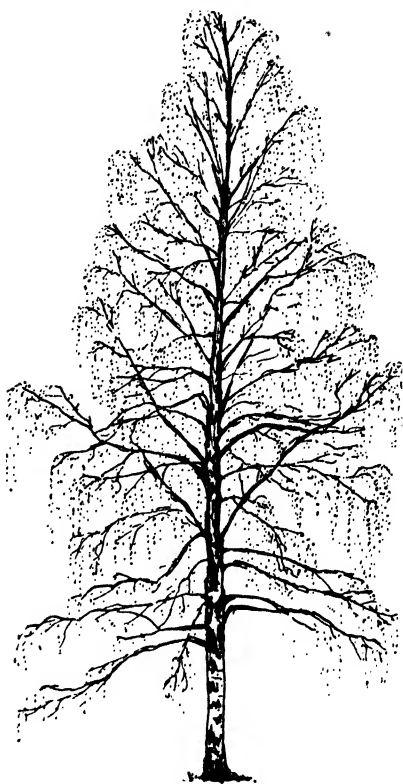


FIG. 168.—*Betula alba*, silver birch. Winter aspect showing pyramidal development of the branches.



openings. An interesting comparison may be made between such a winter bud and a tulip bulb, also a winter bud though formed underground. The similarities are obvious, the main difference

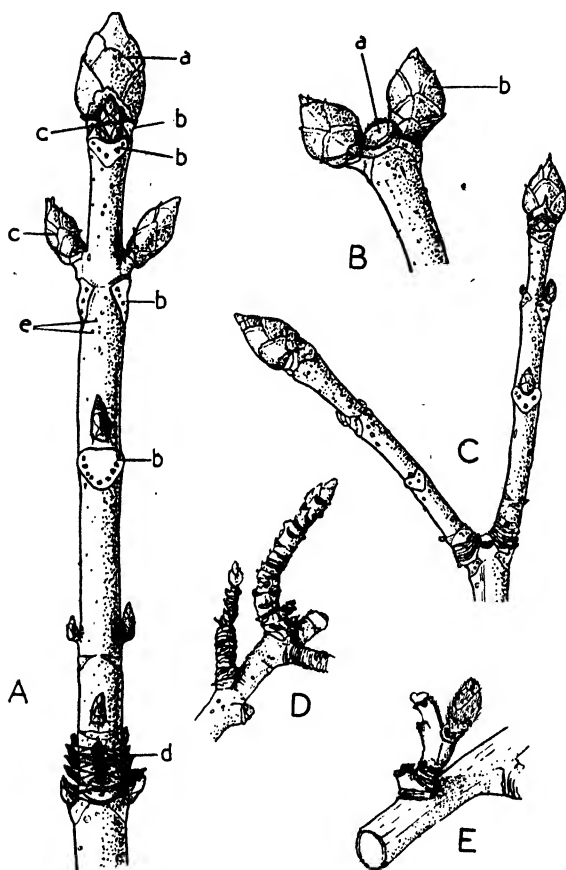


FIG. 169.—Winter twigs. A, horse-chestnut; *a*, terminal bud; *b*, leaf scars showing positions of vascular bundles; *c*, lateral buds; *d*, ring scar with dormant lateral buds; *e*, lenticels. B, horse-chestnut twig that flowered in the preceding season; *a*, inflorescence scar; *b*, lateral bud. C, similar twig one year later; both lateral buds have carried on active growth. D, apple spurs, i.e. short shoots with crowded leaf and ring scars. E, flowering bud swelling. All  $\times \frac{1}{2}$ .

being that the tulip has its reserves in the bulb scales themselves, whereas the bud draws on the reserves in the internodes supporting it. Immediately behind the bud are two scars on opposite sides of the stem and similar scars are repeated down the twig at intervals in an alternating arrangement (Fig. 169 Ab). They are the leaf scars

and are covered by a corky layer in which five or seven dots are visible near the lower edges. These are the scars of the vascular bundles, which passed out into the shed petiole and were finally sealed off. In the axils of the leaf scars are dormant lateral buds (Fig. 169 Ac). Between the nodes, with their alternating pairs of leaves, are long internodes covered with a brown corky surface interrupted by minute vertical slits, the lenticels. Three or four

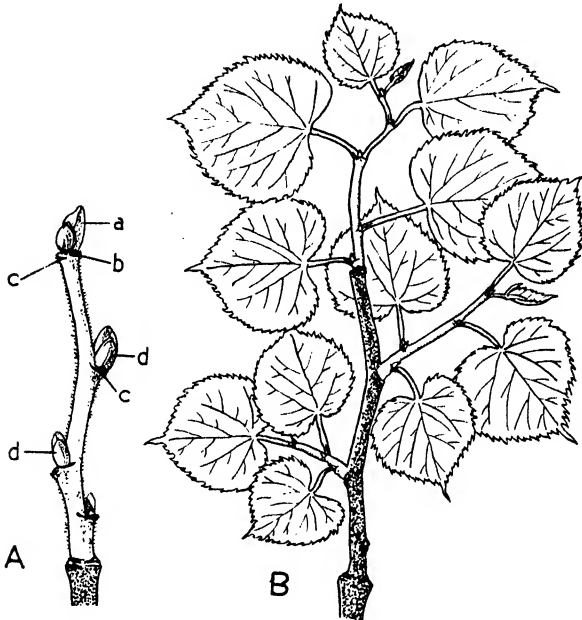


FIG. 170.—*Tilia cordata*, lime, twigs in winter and summer. A, winter aspect; a, lateral bud which will continue the twig's growth in length; b, scar of terminal bud; c, leaf scar; d, other lateral buds. A ring scar is shown at the bottom and growth of the previous year is heavily shaded. B, the same in summer, all the lateral buds having made new growth.  $\times$  about  $1/4$ . After Troll.

internodes behind the terminal bud, a ring scar is visible (Fig. 169 Ad) where the bracts of the previous terminal bud were shed. The interval from the current terminal bud to the scar of the previous one indicates the growth of the year past. Very similar arrangements on a somewhat smaller scale can be studied in the sycamore.

A lime twig (Fig. 170 A) examined similarly shows a series of lateral buds borne singly at the nodes, successive buds being on opposite sides. If the bud nearest the tip is examined it will be found to have two dissimilar scars, one on either side of it. On one side it

has a leaf scar like all the subsequent buds, which suggests that, in spite of its terminal appearance, it is really a lateral bud, borne in the axil of the nearby leaf scar. This is confirmed by the scar on its other side which shows where the true terminal bud has withered away. In the following spring this lateral bud would carry on the growth in the old line. At the same time some of the lower laterals might also sprout and form side shoots (Fig. 170 B). In lilac (*Syringa vulgaris*) twigs also the terminal bud aborts but, as the lateral buds are borne in opposite pairs, two more or less equal shoots carry on the growth in the following season (Fig. 171). If the terminal bud is injured at an early stage or removed by pruning, the inhibition it exerts upon the lateral buds is removed and they begin to grow out as in a sympodium.

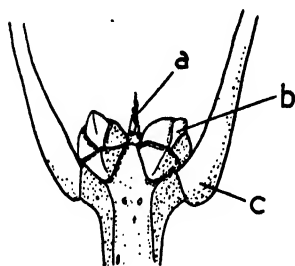


FIG. 171.—*Syringa vulgaris*, lilac, tip of twig in late summer. *a*, remains of terminal bud; *b*, lateral bud; *c*, base of petiole.  $\times 2$ .

In all the foregoing examples the shoots, whether terminal or lateral, all display good extension growth of their internodes during the spring and summer seasons. Some trees, of which apple (*Pyrus malus*) may be taken as an example, produce lateral shoots in which the internodes remain very short. In apples these are produced some way behind the apex and are easily distinguished by their short lengths crowded with leaf and ring scars (Fig. 169 D). In some unknown way the reserves of these twigs are diverted to fruit formation in place of wood formation and, instead of making long woody internodes, they produce flowers followed by the large fleshy fruits. Apples are never formed on main shoots or on lateral long shoots, so the production of spurs (short shoots) is of much importance and is encouraged by such means as suitable pruning. Even more highly condensed shoots are found in *Pinus* whose leaves are produced in tufts, so crowded are they on the minute short shoots.

### Secondary Meristems

It is evident that in the building up of the massive trunk and branches of a large tree much hard and mechanically strong tissue has been formed. To a lesser extent the same must apply to shrubs. These tissues are not produced from the primary meristems of the shoots, but by the activity of secondary meristems, the most

important of which is the *cambium*.<sup>1</sup> This occurs in the vascular bundles of dicotyledons as the portion of the procambial strand that remains undifferentiated into either xylem or phloem (Fig. 149 g, p. 236). In sunflower and similar stems, the cambium forms a broken ring in cross-section and, when secondary growth is about to begin,

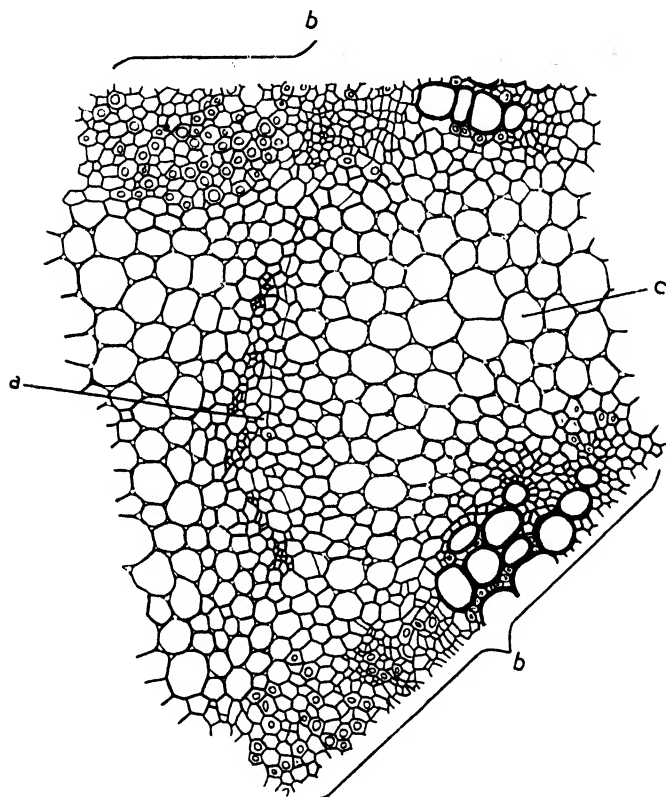


FIG. 172.—*Helianthus annuus*. T.S. medullary ray between two vascular bundles, showing secondary thickening about to begin. *a*, interfascicular cambium; *b*, vascular bundles; *c*, medullary ray joining the pith.  $\times 100$ .

ray cells between the bundles regenerate (Fig. 172 *a*) and so complete the cambial ring, i.e. cylinder in the solid. The bundles of monocotyledons are closed, i.e. they differentiate fully into xylem and phloem in the primary structure, leaving no cambium (Fig. 154, p. 241). In most species no regeneration occurs and they have normally no secondary growth. The seedlings of the tree-forming angiosperms,

<sup>1</sup> Latin, exchange.

on the other hand, have cambia which become active at an early stage and make vigorous secondary growth. The gymnosperms behave similarly, being nearly all trees. Cambia also occur between the xylem and phloem of roots.

Cambial cells are thin-walled, rectangular in cross-section (Fig. 149 g) and elongated longitudinally. They are wider tangentially than radially and have oblique end walls (Fig. 173). The regenerated cambial cells of the rays have quite a different shape. They remain isodiametric and divide more slowly (Figs. 173 and 175).

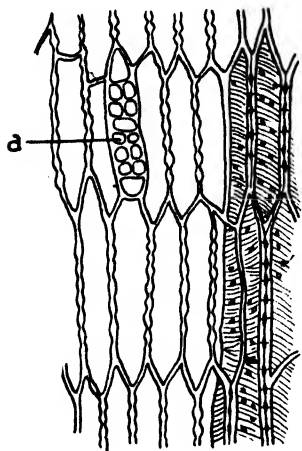


FIG. 173.—Tangential L.S. of cambium of *Cytisus laburnum*. On the right the section is running into the fibre-tracheids of the latest-formed xylem. The beading on the vertical walls of the cambial cells is characteristic. *a*, cambium of a secondary ray, i.e. a small ray which does not connect with the pith. After de Bary.

Another secondary meristem, the *phellogen*,<sup>1</sup> arises in the stems and roots of woody plants. It is formed by regeneration of a layer of the cortex, usually one immediately below the epidermis, but is sometimes deeper seated and may even lie in the pericycle. It forms the secondary covering layers or cork.

Other cambia may be regenerated and cause special local growth. A notable example is afforded by the wound cambia that are formed when young tissues are lacerated (Fig. 174).

### Secondary Thickening

The sycamore (*Acer pseudoplatanus*) develops its secondary tissues as follows. Other woody dicotyledons behave in a generally similar fashion but there are many differences of detail and every wood has its own characteristics. When secondary growth begins, elongation of the shoot is already complete and the new growth is a growth in thickness. It is brought about by divisions of the cambial cells, which cut off new xylem elements inwards and new phloem elements outwards. The cambium proper is only one cell deep in the radial direction (Fig. 175), the same cell cutting off daughter cells both inwards and outwards. When growth is rapid there is a zone of tissue mother cells on either side of the cambium differentiating into

<sup>1</sup> Greek φελλός (phellos), cork, and γεννάω (gennaō), produce.

xylem inwards and phloem outwards. The stages of the development may be followed step by step in a transverse section across the cambial zone (Fig. 175). On the inside the xylem mother cells form closely pitted vessels (Fig. 175 b) and fibres (Figs. 176 and 177). Around the vessels are sheaths of "substitute fibres" which retain their protoplasm and store starch. These may divide while still undifferentiated by horizontal walls and so form a vertical series of parenchyma cells as part of the sheath round a vessel. Their walls become thick and

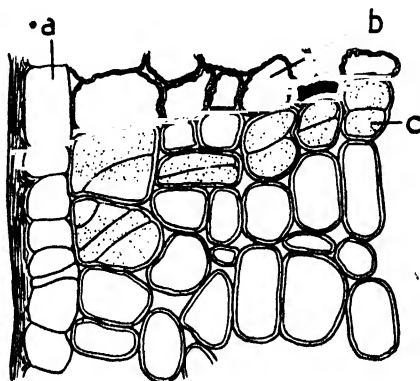


FIG. 174.—Wound cambium in a lacerated leaf of *Clivea miniata*. *a*, epidermis; *b*, dead cells; *c*, regenerating and dividing cells (cambium).  $\times 180$ . After Molle.

lignified like those of fibres, but have large bordered pits where they abut on vessels.

In the phloem, wide sieve-tubes and companion cells are differentiated (Fig. 175). The arrangement of the tissues at the end of the first season of growth is indicated in Fig. 178 A.

After a period of dormancy during the winter, secondary growth is resumed in the next and following springs on much the same lines. The continual expansion of the stem, due to xylem formation, causes the delicate phloem outside to be crushed against the pericycle fibres and disintegrated. The remains are finally dissolved away and disappear completely. Secondary phloem formed in later years develops bands of thick-walled phloem fibres between which the groups of delicate sieve-tubes and companion cells are supported.

### Secondary Rays

A further consequence of the increasing size of the xylem core is that the cambial cylinder on its surface is continually being enlarged.

The width of the cambial cells in the tangential direction remains the same, so it is evident that the number of them round the stem must increase. This seems to come about to some extent by the formation of new walls that are almost horizontal at first but later grow into a radial longitudinal position, but the formation of new rays is also important. A single elongated cambial cell forms a vertical file of ray initials by horizontal divisions. These may divide

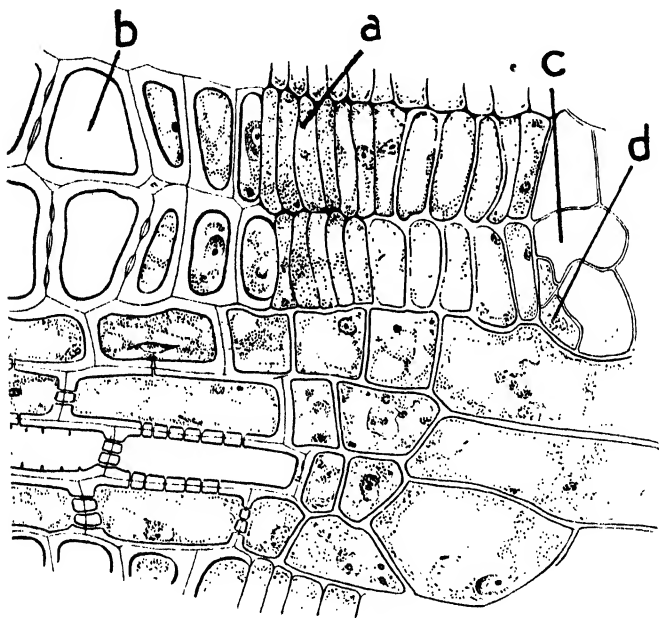


FIG. 175.—*Acer pseudoplatanus*. T.S. cambial zone of a young twig. *a*, cambium with undifferentiated tissue mother cells on either side; *b*, vessel; *c*, sieve-tube; *d*, companion cells. Medullary ray below.  $\times 550$ . After James and Baker.

radially so that the ray becomes several cells wide (Fig. 173 *a*). In the xylem such a secondary ray may remain narrow, but in the phloem, which is being stretched over the surface of the wood, it usually widens out by further radial divisions of its cells and their expansion tangentially.

The rays come into contact with the sheaths of living cells round the groups of vessels (Figs. 176 and 177). Owing to their rounded corners their cells leave spaces that are continuous from the lenticels (p. 274) in the corky surface, even through the cambium (Fig. 179). There are thus continuous air passages and a network of living cells throughout the wood.

*Annual Rings*

The concentric rings shown by the wood of a tree stump just after felling are familiar. They result from the periodic rhythm of the wood's growth. In the spring when the annual growth cycle begins,

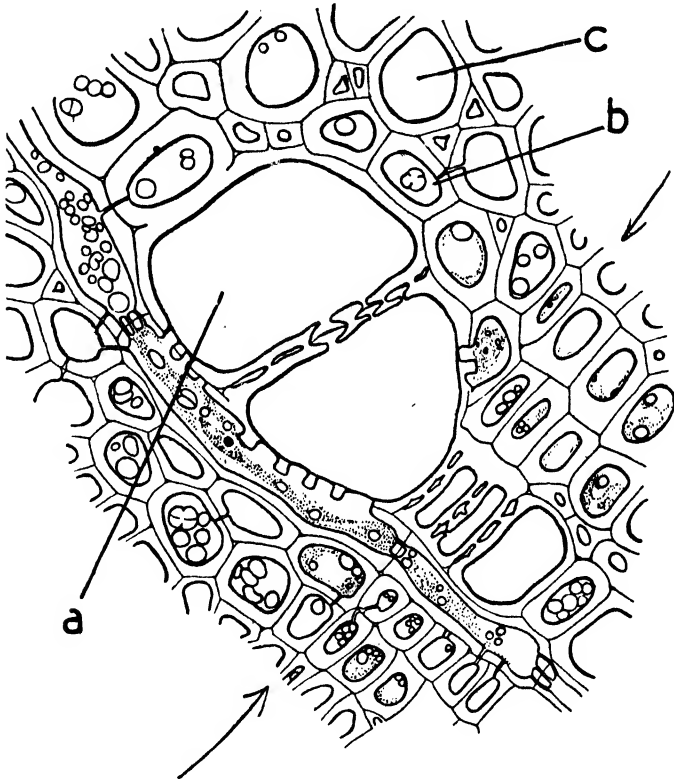


FIG. 176.—*Acer pseudoplatanus*. T.S. of a set of vessels and surrounding cells. *a*, vessel with a ray, one cell wide, adjoining; *b*, substitute fibre with starch; *c*, fibre. The arrows show the line of division between one year's growth and the next.  $\times 600$ . After Baker and James.

the vessels formed are relatively wide and the walls of the fibres thin. This development is correlated with the unfolding of the new season's leaves and the rapid transpiration resulting. As the season advances, the vessels become narrower and fewer and the fibres correspondingly more numerous and thick-walled. Much of the carbohydrate found in the leaves is used in this way and more is deposited as starch in the parenchyma and "substitute fibres." Growth comes to



a complete stop during the winter so there is a sharp line of demarcation between the close texture formed at the end of the season and the porous texture that is laid down against it in the following spring (Fig. 176). The contrast gives rise to the annual rings that are visible

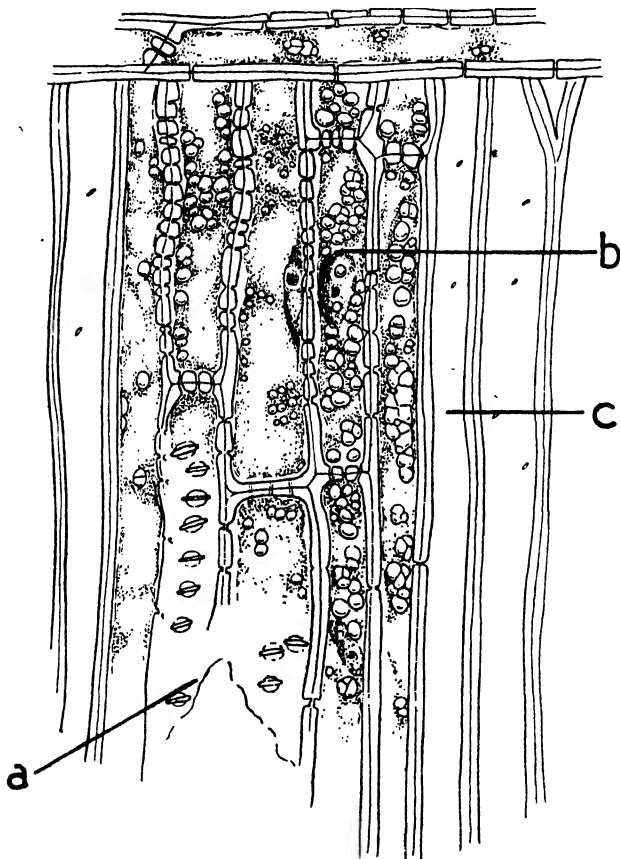


FIG. 177.—*Acer pseudoplatanus*. L.S. of tissues surrounding a vessel. *a*, part of vessel wall with bordered pits; *b*, substitute fibres with living contents and starch grains; *c*, fibres.  $\times 500$ . After James and Baker.

even to the naked eye (Fig. 178 C). The age of a branch or of the tree as a whole can be estimated by counting the annual rings. A check to growth, such as follows a severe midsummer drought, or extensive defoliation by caterpillars, may be followed by the unfolding of a fresh set of leaves and give rise to a second ring in one year.

*Sapwood and Heartwood*

The xylem tissues are liable to slow changes even after they have been fully differentiated. The contents of the living cells slowly die

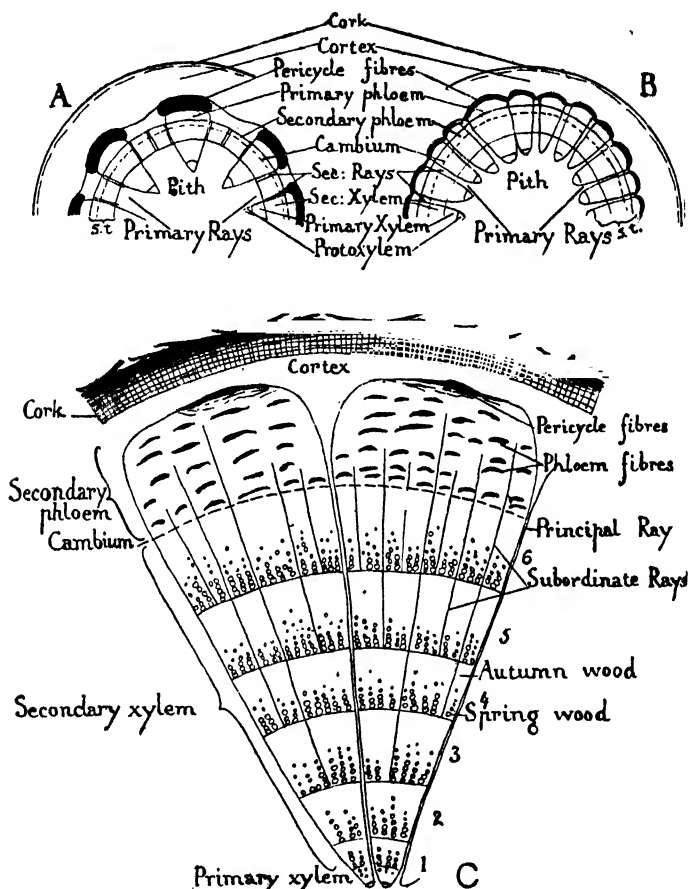


FIG. 178.—Diagrams of secondary thickening in a woody stem. A, cross-section of a young stem in first year of thickening. The bundles are separated by broad medullary (primary) rays until the interfascicular cambium bridging the rays begins to form xylem and phloem. B, the same in the second year of thickening; the primary rays are now narrow. C, part of stem after six years of thickening. Subordinate (secondary) rays are formed within the "bundles" where cambial cells change their activity.

off and the water columns in the vessels break and are to some extent replaced by air. Obscure changes also go on in the lignified walls; they become harder and may become darker in colour. This color-

ation goes to much greater lengths in other woods than in sycamore, reaching its extreme in the almost jetty blackness of ebony. This hardened wood is the heartwood; it no longer serves as a water-conducting tissue and its service to the plant is purely mechanical. It acts as a central supporting pillar or skeleton. It often becomes impregnated with toxic substances that preserve it from fungal and other attacks. Trees like willows—in which such substances do not

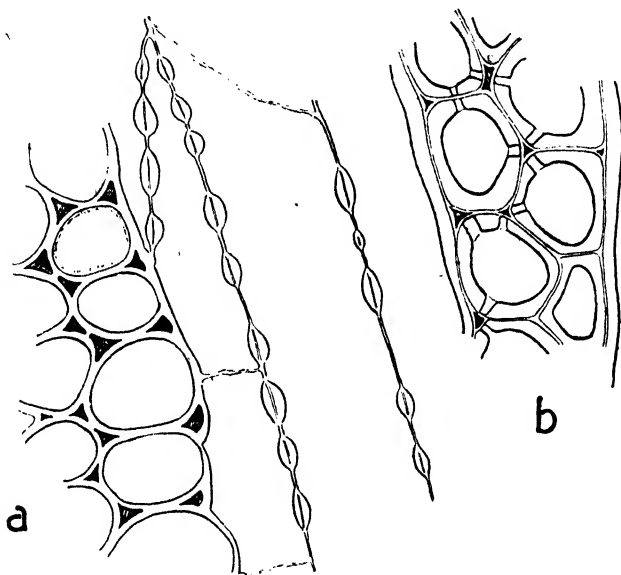


FIG. 179.—*Acer pseudoplatanus*, tangential L.S. of a piece of cambium. *a*, ray initials on the left and normal cambial cells on the right; *b*, ray initials. Intercellular spaces are shaded.  $\times 550$ . After James and Baker.

form in the heartwood—are liable to rot at the centre as is so often seen in pollards. The hard resistant type of heartwood is the desirable wood for building, furniture making and so on, because it does not warp by losing a lot of moisture during seasoning, and is also most durable when dry. The fine regular grain and resistant texture of sycamore wood makes it much valued for cabinet making and allied purposes.

The wood near the cambium which still has its living contents and is still conducting water is the sapwood. It forms a belt of more or less constant width, being continually added to from the cambium outside as it passes into heartwood on the inside.

### Cork Formation

The phellogen of sycamore, like that of most angiosperms, arises immediately below the epidermis. The cells of the outermost layer of cortex perform two tangential divisions, cutting out the phellogen cell between them. The phellogen goes on dividing, cutting off a regular series of cork cells on the outside, and may form a secondary cortex or phelloderm inside. The cork cells are very regular in shape. They are rectangular or almost square in cross-section (Fig. 180) and the same in vertical section. They do not round off at the corners,

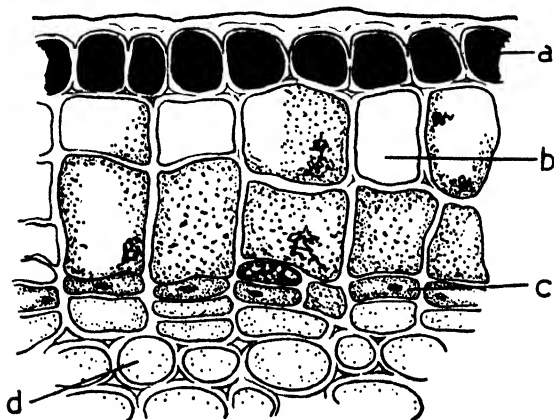


FIG. 180.—*Acer pseudoplatanus*, young phellogen in T.S. internode of stem. *a*, epidermis; *b*, cork cells; *c*, phellogen; *d*, cortex.  $\times 600$ .

their middle lamellæ holding them securely together. They are therefore cubical in shape, or some near approximation to it.

The middle lamellæ and the first layer of cellulose thickening remain unchanged in the cork cells, but then a layer impregnated with suberin is laid down. This is impervious to water and to dissolved materials, so the cell contents die soon after its formation. The last wall layer deposited may be free from suberin and consist only of cellulose again. Brown pigments are usually formed both in the walls and in the cell cavities. An insulating layer several cells thick is thus built up. It is impervious to gases, water vapour, insects and fungal hyphæ and replaces the epidermis which, being isolated outside it, soon dies off. It is perforated here and there by lenticels, which are visible to the naked eye externally as minute dots (Fig. 169 Ae).

*Lenticels*

Phellogen activity often appears first underneath a stoma (Fig. 181 A), and is followed by very active production of cells in the outward direction. Unlike the normal cork cells, these round off at the corners and form a loose powdery tissue whose increase forces off the epidermis, leaving an open break filled only by the loose, brown cellular powder (Fig. 182). Even the phellogen cells appear to have slightly rounded corners in this region so that air spaces are continuous right into the interior of the plant.

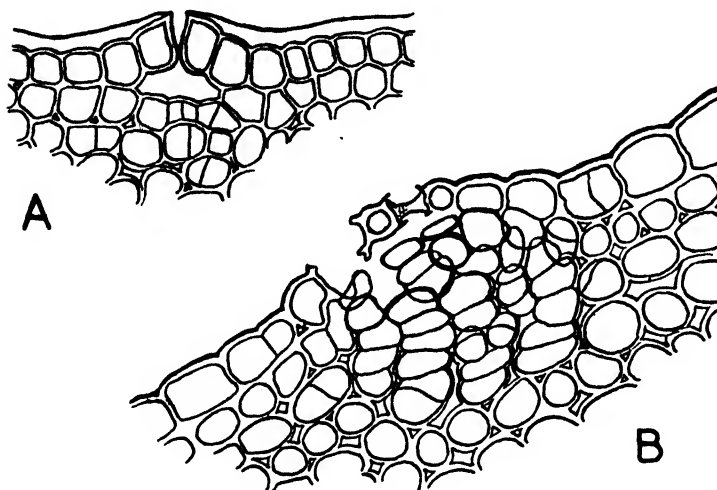


FIG. 181.—Early stages of lenticel formation in internode of *Betula alba*. A, cell divisions starting in cortex below stoma. After de Bary. B, production of loose cells bursting off the epidermis. After Eames and MacDaniels.

*Bark*

The original phellogen does not remain active throughout the life of the tree. After some years it stops dividing and a new phellogen is formed in a deeper layer of the cortex. This cuts off all the outer tissues including the original phellogen and its cork and the process may be repeated later by a third and further phellogens cutting deeper into the tissues of the cortex, or even of the secondary phloem. The zone of functional phloem, the "inner bark," thus remains more or less constant in width, being reduced on the outside by phellogen formation and renewed on the inside by the activity of the cambium. In an old tree-trunk the functional conducting tissues are limited to a narrow zone between the outer bark and the heartwood.

The bark of different trees varies characteristically in appearance. Some have smooth bark that flakes off in plates, like the planes (*Platanus* spp.) or in even larger and smoother sheets, like silver birch (*Betula alba*). This is because their phellogens, and consequently the cork they produce, are uniform and parallel for large tracts of the stem's circumference. Others, like oak and elm (*Quercus* spp. and *Ulmus* spp.) are rugged, with the hard bark splitting and coming off in chunks. They have irregular, curved phellogens that may even intersect one another.

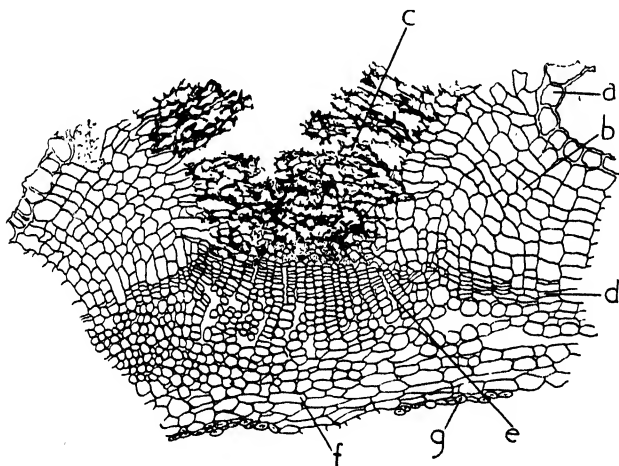


FIG. 182.—Mature lenticel of *Sambucus nigra*. *a*, epidermis; *b*, cork; *c*, powdery tissue; *d*, phellogen; *e*, intercellular spaces in phellogen below the lenticel; *f*, cortex; *g*, pericycle fibres.  $\times 66$ .

The cork of everyday use is obtained from the bark of *Quercus suber*, an evergreen tree of the Mediterranean region. The first formed bark is rough, but when this is stripped away a very thick and uniform growth is made from a new cork cambium arising from deep-seated tissues. This is stripped after about nine years' growth when it may have achieved a thickness of an inch or more. It is boiled to soften it so that it can be pressed into flat sheets, and is then cut as required. The dark streaks are the lenticels. They penetrate the thickness of the cork and render it porous. Bottle-corks are cut at right angles to the lenticels, i.e. vertically in the thickness of the cork and are gastight and watertight as a result. There is obviously a limit of size beyond which a cork cannot be obtained. Wider bungs can be made by cutting with the grain. These are called

shives and are pervious to gas and water. Cork has many other useful properties. It is mechanically tough, chemically very resistant: it is light, hard to wet and a non-conductor of heat. These properties make it useful to man for a wide range of uses, as well as to the plant that formed it.

### *Abscission Layers*

As the season advances the green surface of a new sycamore twig turns dull owing to the beginnings of cork formation under the epidermis. The petioles of the leaves, on the other hand, remain

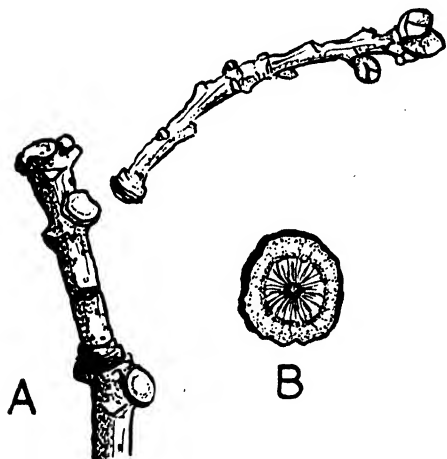


FIG. 183.—Abscission layers in oak twigs. A, on the right a twig that has been cut off, and on the left a twig showing surfaces where others have been shed. About nat. size. B, abscission surface showing wood at centre and corky tissue round. The powdery abscission cells have dropped away.  $\times 2$ .

bright green as they form no cork. Quite a sharp line of demarcation can be seen and this is the place at which the leaf will be cut off from the stem. A layer of parenchyma, the abscission layer, stretches across the petiole at this point, penetrated only by the vascular tissue which has less collenchyma and fewer fibres here than in the petiole generally. In this layer of parenchyma, towards the end of the season, the calcium pectate of the middle lamella goes into solution in an excess of pectic acid. The middle lamella breaks down, the cells cease to adhere and the weight of the leaf causes it to drop away. Before this happens, the cells immediately below the abscission layer on the stem side have become suberised so that when the leaf drops

away a continuous cork layer covering the leaf scar is already in existence.

Other abscission layers are formed that cut off the remains of large inflorescences, as in horse-chestnut (Fig. 169, p. 262), fruits like apples and pears, and even small branches. This happens in black poplars (*Populus serotina*) and oaks (Fig. 183). The base of the

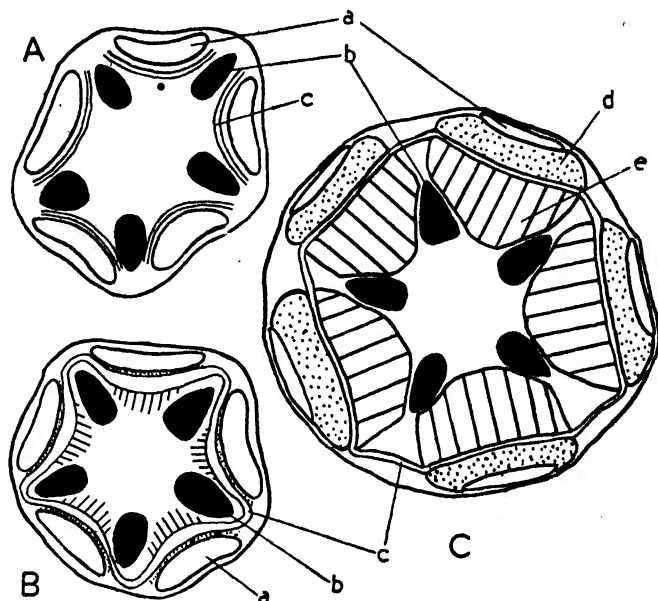


FIG. 184.—Diagrams of secondary thickening in a woody root. A, primary structure, cambium appearing. B, after a year's thickening. C, after two years' thickening; a, primary phloem; b, primary xylem; c, cambium; d, secondary phloem; e, secondary xylem.

branch swells out owing to the formation of a layer of loose tissue instead of wood. Finally the branch drops away and the scar develops cork on its surface. Branches shed in this way have usually borne catkins (staminate inflorescences).

### *Secondary Thickening in Roots*

Trees and shrubs that build up large shoot systems also have massive roots to support and supply them. These are developed in similar fashion by the activity of a cambium and phellogen, but with certain differences. Only a general outline is given below.

The procambial strands of angiosperm roots differentiate fully in



the primary root structure (Fig. 160, p. 250): no meristematic tissue is left to become a secondary meristem. There is always, however, a small tract of parenchyma between the arms of the xylem and the adjacent strands of phloem, and in this a cambium regenerates. It appears first inside the phloem strands (Fig. 184 A), and gradually joins up over the protoxylem points. As in stems, it proceeds to cut off secondary xylem elements inwards and secondary phloem outwards. Opposite the protoxylems it usually cuts off parenchyma to form rays. Owing to more rapid division opposite the primary phloem groups, the originally wavy course of the cambium soon becomes a regular circle in cross-section and thereafter the structure appears superficially similar to that of a stem. The different arrangement at the centre (Fig. 184 C) makes it easy to recognise a cross-section of a root even after thickening has gone on for several years. The character of their secondary wood is also different from that of stems. It usually has more numerous wide vessels, fewer and thinner-walled fibres and, since root growth is less seasonal than that of stems, there is no appearance of annual rings.

The primary phloem soon becomes crushed and disorganised by the pressure of the enlarging xylem and is replaced by the secondary phloem which, besides sieve-tubes and companion cells, may also develop groups of fibres.

*Cork Formation.* The phellogen of the root arises in the pericycle. In many roots the endodermis has already become corky when this happens and the cortex has already shrivelled away. This is why the roots look thinner and browner some way behind the tip than they do in their primary regions. The activity of the phellogen, when it appears, leads to cork formation in similar fashion to that of the stem; but there are no lenticels. The cork of the roots splits and is replaced by new cork from new phellogens forming in the secondary tissues.

#### TRANSLOCATION

Most of the organic materials of the higher plants are synthesised in the leaves; but the main sites for their utilisation are the meristems, both primary and secondary, of roots and stems. By some means the sugars and proteins formed in the leaves must be moved to the meristems and further quantities must find their way to storage organs above and below ground. This movement is called translocation, and it goes on continuously by day and by night. During the day a leaf's photosynthesis exceeds its translocation and sugar or

starch heaps up, but translocation continues throughout the night and the sugar and starch content of the leaf diminishes. Starch is not translocated as such, but is first hydrolysed back to sugars; and it is a general rule that only soluble substances are transported.

The principal path of translocation is the phloem, and in all probability the sieve-tubes. It is not safe to jump to the conclusion that they are necessarily the path of transport just because their elongated shape and perforated sieve plates suggest it. Tests show also that they do contain sugars and proteins in abundance. The most important observation is, however, that removal of the phloem brings translocation to a standstill. This is most conveniently done in woody stems whose phloem is limited to a narrow ring outside the wood. If a ring of bark including the phloem is cut away to the cambium the leaves above do not wither because water continues to pass upwards through the young xylem. Plastic materials cease to pass downwards, however, and may accumulate above the ring. This may even produce additional growth which becomes obvious as a swelling above the obstruction. As a result of such experiments, often carried out with many precautions, it seems fairly sure that translocation occurs by way of the sieve-tubes. The mechanism of this movement is still very uncertain. Generally, translocation of a substance takes place from a region of high concentration such as the leaf, to one of low concentration such as a meristem, where it is being used up. Obvious and important exceptions to this rule are the movement of sugars into ripening fruits and beetroots where their internal concentration is already very high. The rate of translocation is many times too fast for it to depend on diffusion.

## Practical Work

### WOODY SHOOTS

- (1) Make a drawing of a **winter twig** of horse-chestnut or sycamore showing two or three years' growth. Label the *terminal bud*, *lateral buds*, distinguishing *dormant buds*, *bud scales*, *leaf scars*, *bud-scale scars*, and *lenticels*. Indicate each season's growth. Dissect out a large terminal bud and distinguish the *bud scales*, young *foliage leaves* and *inflorescence bud*, if present.
- (2) Make a drawing or diagram of a horse-chestnut or sycamore **twig that has sprouted** and label the parts.
- (3) Make a similar examination of lime and lilac twigs.

### SECONDARY THICKENING OF STEMS

- (4) Examine a **transverse section** of a sycamore twig about three years old. A preliminary examination with a hand lens will be helpful. Then make an outline

diagram with the help of the low power (cf. Exp. (5), p. 259), labelling *cork*, *phellogen*, *outer cortex*, *inner cortex*, *pericycle*, *secondary phloem*, *cambium*, *secondary xylem* with *annual rings*, *principal rays*, *later-formed rays*, *primary xylem* and *pith*.

(5) Examine a **radial longitudinal section** of the same organ. Identify the tissues by comparison with the transverse section. Make drawings of groups of cells from the *cork*, *cortex*, *phloem*, *primary* and *secondary xylem*, including *rays* in both longitudinal and transverse sections.

(6) Examine with the naked eye and a hand lens a **wedge of wood** cut to show transverse, radial and tangential surfaces as well as the bark. A segment of oak, smoothed and polished, is excellent for this purpose. Make the following observations:

*Transverse*: *Annual rings*, large *spring vessels*, masses of *fibres*, *secondary rays*, functional *phloem* (yellow-brown) and *outer bark* consisting of *cork* and dead *phloem*.

*Radial*: *Annual rings*, *spring vessels*, *sinuous rays* (the "silver grain"), *bark*.

*Tangential*: *Rays*, note vertical extent.

The distinction between heartwood and sapwood can be observed on both transverse and radial sections.

(7) Make a similar observation of cork oak (*Quercus suber*), birch (*Betula alba*) and sycamore.

#### CORK FORMATION

(8) Examine a **first-year branch** of elder (*Sambucus nigra*). Some way behind the tip notice how the fresh green colour of the stalk turns to grey where cork is being formed *under* the epidermis. Note that the petioles do not change colour. Farther back note the splits in the first-formed cork as the stem thickens. The numerous brown pustules are lenticels. Break the branch across and strip away the cork; note the green cortical cells beneath, and the depression below the lenticels.

(9) Mount a flake of **cork** from a young elder stem in dilute glycerine and examine under the microscope. It is still only one cell thick. Note and draw the isodiametric shape of the cells, the *middle lamella* leaving no intercellular spaces and the thickenings of *suberin*. Treat with Sudan IV or chlor-zinc-iodine. If a *lenticel* is present in the flake note that its cells are browner and beginning to separate from one another.

(10) Examine and draw a prepared **transverse section** of elder bark. Label *cork*, *phellogen*, *phelloderm*, *cortex*, *lenticel* and its powdery cell tissue.

#### SECONDARY THICKENING OF ROOTS

(11) Examine a prepared transverse section of an old root. Make a diagram showing the distribution of the tissues including *cork*, *secondary phloem*, *secondary xylem*, *rays* and *primary xylem*. Label the parts.

## GROWTH, DEVELOPMENT AND IRRITABILITY

*The Growth Cycle*

It has been shown in the previous chapters that plants grow by addition of new cells at primary and secondary meristems. Although these are separate and distinct regions of the plant, growth is not disjointed and haphazard. The plant grows as a whole and exhibits a definite cycle of growth rates. Taking the increase of substance exclusive of water (dry weight) as a criterion of growth, it is found to increase slowly at first, then more rapidly and then slowly again

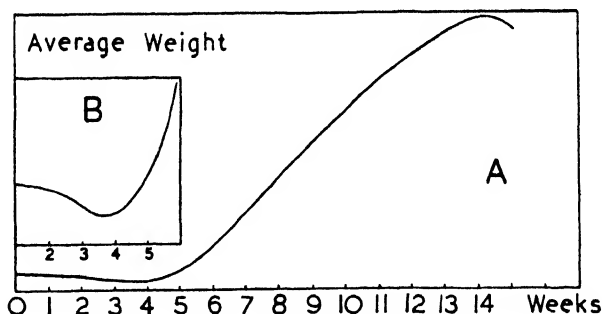


FIG. 185.—A, graph of the increase in dry weight of a maize plant to its maximum in 14 weeks. B, early part of graph A with the vertical scale enlarged. The drop at first occurs while the seed is germinating and before the leaves are able to photosynthesise.

until growth stops altogether. The weight of an annual plant increases according to a graph of the kind shown in Fig. 185. Separate parts, such as developing fruits, follow a similar growth curve. Root systems may show a succession of such curves, as first the main root, then the laterals, tertiary roots and so on are produced in waves. Perennial plants may show a succession of such phases as the growth seasons follow one another.

The early part of this curve is a close approximation to the curve of compound interest, and is followed so long as the initial meristems can grow freely, unrestricted by shortage of food or other interference. As the plant grows the meristems become a progressively smaller part of it, and it is evident that restrictions begin to slow down their growth rate, but what the restrictions are and how they operate is still uncertain.

Growth does not follow a mere course of increasing bulk; qualitative changes are also taking place. Most noticeable of all, the plant sooner or later changes from producing foliage to producing flowers. When this happens it has built up a reserve of food that is utilised in flower and fruit formation. In annuals, this commonly takes place towards the end of the growing season. Many apple trees notoriously lay up food reserves in one year and flower and fruit freely the next; and beech trees come into full fruiting about once in eight years. The accumulation of food does not in itself initiate flowering. It is coming to be more and more accepted that the leaves produce a flowering hormone which, when it has accumulated enough in the meristems, starts them on their new kind of development.

### *Vernalisation*

The duration of the vegetative phase of development and the stage at which flowering supervenes depend to a remarkable extent upon the experiences of the young plant in its very earliest stages, and particularly upon the temperatures to which it has been exposed. Some sub-tropical plants flower very much earlier if they have experienced warm weather during their germination period. Conversely, some temperate plants flower much sooner if exposed to cold, only a degree or so above freezing, during germination, even though it retards growth at the time. A variety of rye that has been carefully investigated, normally comes into ear when it has formed twenty-five leaves. By exposing it to cold during germination it can be made to flower after forming only seven leaves. The time taken is reduced from about 140 to 100 days though, under cold treatment, there may be little growth for the first half of the time. This is termed vernalisation and one explanation is to suppose that it increases the accumulation of flowering hormone in the meristems, so that the critical concentration is reached sooner than usual.

### *Photoperiod*

Another circumstance which greatly affects a plant's time of flowering is the length of day to which it is subjected. The flowering

of "short-day plants" is accelerated if they are grown in day lengths of twelve hours or less, whereas "long-day plants" flower soonest with continuous light periods of sixteen hours or more. Greenhouse chrysanthemums and runner beans are well-known short-day plants. Long-day plants are more numerous and include the majority of species investigated. About one-third appear to be "day-neutral" and show no response to such adjustments. The classification into long- and short-day is arbitrary, and it seems possible to find a plant with a day-length optimum of any intermediate length. Many curious but unexplained facts have been discovered about photoperiodism; but perhaps one of the most interesting is that it can be used as a method of vernalisation. The plant is highly sensitive to day length for a short time after its first leaves have been spread, and the day length it experiences at that time will affect its time of flowering irrespective of what happens later. As day-length changes so much during our spring season, this is obviously a weighty factor in the development of our annuals.

### *Nutritional Factors*

Growth is dependent upon metabolism for its raw materials and may be much affected by the factors controlling it. The accumulation of carbohydrate by photosynthesis is a pre-requisite without which there can be no growth; but it needs to be blended with other essentials. Supplies of nitrogen have to be obtained from the soil before protein synthesis can occur; and a normal and vigorous growth results only if the two materials are on hand in suitable proportions. Nitrogen-poor soils and hot sunny seasons both lead to hard and woody plants of stunted growth and premature flowering. A large excess of nitrogen in the soil, whether produced naturally or by artificial fertilisation, delays flowering and tends to a very lush growth of leaves. The large leaves may be able to rectify the balance by their active photosynthesis, so that the eventual flowering and fruiting may be greater than that of the precocious, nitrogen-starved plants.

### *Correlation*

The different parts of a complex plant exert mutual influences upon one another, and the form and development of the plant as a whole may be very much influenced by this interplay. One of the most obvious and familiar examples is the action of the terminal bud in suppressing the growth of axillaries. If it is destroyed or withers

away, the nearest laterals, and perhaps others as well, become active (cf. p. 264). The origin of the inhibition appears to be in the young leaves of the apex, not in the meristem itself, and is transmitted as a hormone or hormones to the inhibited buds.

Another familiar example of correlative inhibition is revealed when a piece of stem is cut and the end placed in wet sand. After a short interval adventitious roots are formed at the lower end, which would not have been formed by the cells originating them if left in their normal position. In other words, the removal of the original root system has taken away some influence that prevented these cells from forming other roots when it was present. The formation of roots on such a "cutting" is on the other hand accelerated by the presence of active buds higher up the stem. This is because they are sending down a hormone that promotes the growth of the new roots. The same effect can be obtained artificially by soaking the cut end in a very dilute solution of this hormone,  $\beta$ -indolylacetic acid.

The co-ordination of a plant's growth is thus very largely dependent upon hormones produced in one part suppressing or accelerating the growth of other parts. Much also depends upon the fact that different parts tend to have their own characteristic growth rates. Thus, a cypress whose main stem grew three times as fast as its branches would form a narrow cone, and any alteration of the relative rates would alter its proportions. Similarly, the proportions of many plant parts, fruits and the like, are dependent on the existence of characteristic growth rates in different directions. How such relations are determined is not yet known.

### *Growth Hormones*<sup>1</sup>

The best-known plant hormones are the growth substances or *auxins*. They are produced in minute quantities in the growing points of stems and roots and, passing back into the vacuolating zone, control the rate of elongation. A special organ, the coleoptile or modified first leaf of grass seedlings, has been much studied on account of its convenience. It produces auxins in its tip and has a tubular region behind that elongates under their influence. Of the auxins, the best known is  $\beta$ -indolylacetic acid, which can be prepared artificially, the artificial product behaving just as the extracted one. Substances of related chemical composition such as naphthalene acetic acid, often produce similar effects in the plant also. When auxin passes out of the coleoptile tip into its elongating zone,

<sup>1</sup> Greek ὁρμάω (hormao), impel.

growth in length is accelerated. Precisely the same thing occurs if the tip is sliced off and a tiny block of agar jelly impregnated with auxin is put in its place. If the block is fixed to one side, elongation is fastest on that side so that the tip is pushed, or curves, over towards the other. Similar effects occur in stems, but in roots the same auxin retards the rate of elongation.

The action of  $\beta$ -indolylacetic acid is not specific to a single plant, but occurs in all the plants investigated and extends to a curious variety of effects. Besides affecting elongation, it acts as a cambial stimulus, awakening the activity of dormant cambium in the spring, and it favours root production as described above. It tends, probably after conversion into a second hormone, to suppress lateral shoot development and, conversely, *Aster* species with abundant branching have been shown to be poor in auxin. It retards the development of abscission layers, both of leaves and fruits, an observation that has been turned to practical account by spraying apple trees with naphthalene acetic acid to prevent fruit dropping off prematurely. The swelling of fleshy fruits (as well as the fertilisation of the ovule) is dependent upon pollination, and the cause of the swelling has been traced to a transfer of auxin. Artificial application of synthetic growth substances to unfertilised tomato gynæcia will often cause them to start growing. The fruit produced contains no seed since no fertilisation of the egg by sperm nuclei has taken place.

The auxins produce their effects in exceedingly dilute solutions, one part in a hundred-thousand or so, and in higher concentrations cause deformation and death of the tissues. Some plants succumb at lower concentrations than others. The brassicas, the cabbage group and charlock, are killed at much lower concentrations than the cereals. Solutions of synthetic auxins, therefore, find an application as more or less selective weed-killers.

#### IRRITABILITY

Protoplasm, whether in the form of a simple unicellular organism or a complex one, is characterised by the multiplicity of its responses to external stimuli. It also shows frequent changes that cannot be ascribed to any obvious external influence, and which are therefore described as autonomic. Irritability is a name for this extreme reactivity of protoplasm. The energy imparted by the stimulus is only a minute fraction of that involved in the observed response. Since the responses of irritability are always suppressed in the



absence of oxygen, it appears that the difference is made up by aerobic respiration, though by what means is still unknown. Plant responses to stimuli fall under three main headings: taxic, the movement of free cells or cell parts; tropic, the curvature of fixed parts in relation to a unidirectional stimulus; and nastic, movements of fixed parts in response to diffuse stimuli.

### *Taxis*

A familiar example of taxic movement is the movement of free-swimming unicells towards a source of light (Exp. (3), p. 290);

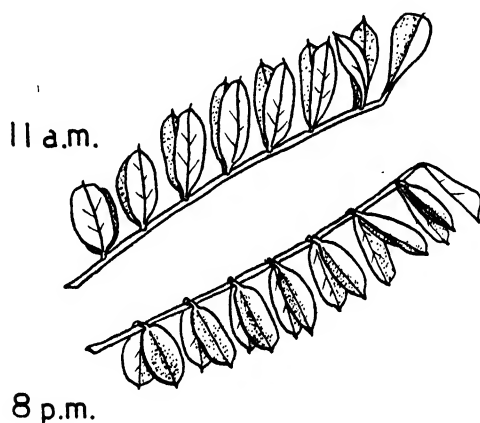


FIG. 186.—Leaves of *Indigofera gerardiana* in morning light and evening dusk. On dull days these leaflets take up an intermediate horizontal position.

it is characteristic of species with eye-spots. The chemotaxis of flagellated sperms has been described on pages 144 and 157. In addition the chloroplasts of palisade cells exhibit movements depending upon the intensity and direction of light. Intense light entering at right angles to the leaf surface causes the chloroplasts to migrate to the vertical walls, but in a moderate light they take up their positions on the cross walls. In ordinary circumstances the abundant reflexion of light from the cell walls in passing through a leaf obscures these responses. The naked protoplasm of Myxomycete slime-fungi flows slowly away from a bright light.

### *Nastic Movements*

The periodic movements of flowers and leaves are mostly of this kind. Many flowers open by day and close at night, exhibiting so-

called sleep movements. Two stimuli, light and heat, are involved. Examples of photonastic movements depending upon light are the opening of daisy-heads (*Bellis perennis*), and the spreading of wood-sorrel (*Oxalis acetosella*), *Mimosa* and *Indigofera* leaves (Fig. 186). The response is different in other plants; light causes the flowers of

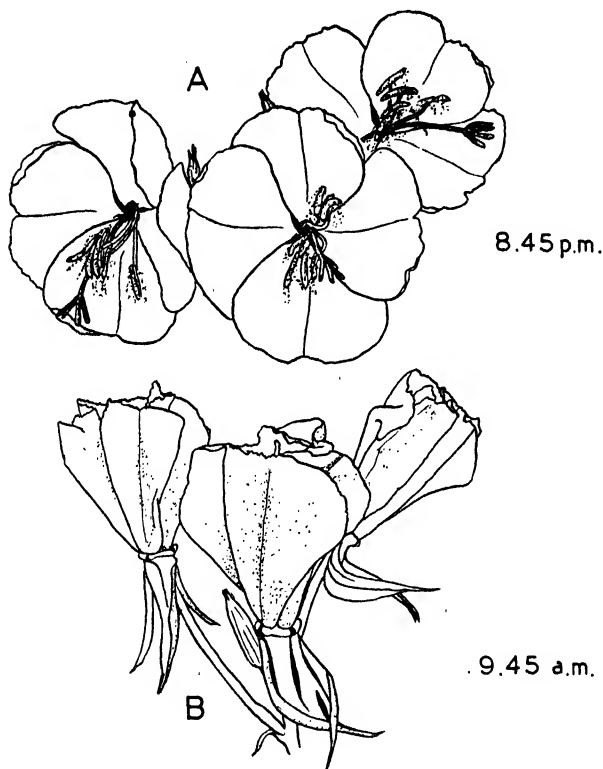


FIG. 187.—Flowers of *Oenothera*, evening primrose, in evening dusk and the light of the following morning.

evening primrose (*Oenothera* spp. Fig. 187) and tobacco (*Nicotiana tabacum*) to close and the leaves of balsam (*Impatiens* spp.) to droop. The flower movements are probably brought about by unequal growth on the two sides of the petals, but the leaf responses result from changes in the turgor of swollen pulvini in the position of hinges.

Flowers may be capable of both photo- and thermonastic movements. Young tulip and crocus flowers held at constant temperature

have been shown to open in response to light and close again in the dark. When kept under constant illumination they opened in warm air and closed in cool.

Stems submitted to variations in light intensity have been shown to exhibit very complex responses in their rates of growth, usually ending with a slight slowing-down of elongation in light. Roots are mostly indifferent to light, but a few show a similar effect.

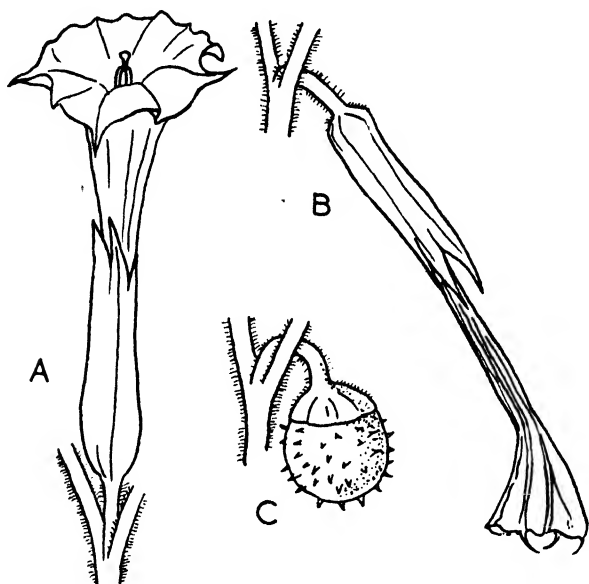


FIG. 188.—*Datura metel*. A, opening flower, negatively geotropic. B, fertilised flower and C, fruit, positively geotropic.

### Tropisms

These are perhaps the most important of the responses of higher plants to stimuli, since they have drastic effects upon their growth and form. They are of many kinds: geotropic in response to gravity; phototropic in response to light; chemotropic in response to concentrations of soil components; hydrotropic in response to moisture and haptotropic in response to contacts. Geotropic and phototropic responses have been the most carefully studied.

**Geotropism.** Stems are as a rule negatively geotropic and roots positively geotropic, growing vertically upwards and downwards respectively. Leaves, lateral roots and branches are usually diageotropic, i.e. they grow horizontally under the influence of gravity.

Some organs change their responses as they develop. Poppy buds are positively geotropic and grow (not hang) downwards; but as the flower opens and the fruit ripens they become negatively geotropic and the ripening capsule stands bolt upright. Converse changes are



FIG. 189.—Broad bean roots placed in the horizontal position after decapitation. A, with no tip. B, with tip replaced. After Snow.

shown by the flowers and fruits of *Datura metel* (Fig. 188). The lateral branches of bindweed (*Convolvulus arvensis*) seedlings are at first diageotropic, then they become negatively geotropic for a time and, after they have penetrated the soil, again become diageotropic and continue to grow as horizontal rhizomes. The result of these responses obviously has a great effect in determining the spread, and hence the nutrition, of the plant (Fig. 106, p. 184).

The geotropic stimulus is effective only in the growing tips of roots, and if they are cut off the power to respond goes with them (Fig. 189), but can be at least temporarily restored if the tip is replaced or by applying an auxinated agar block to the stump. The actual response occurs in the elongating zone, and is due to more rapid elongation of the side of the root that happens to find itself uppermost. The stimulus is thus transmitted from the tip in the form of auxin, which, by some means unknown, becomes unevenly distributed with a lower concentration on the upper surface. Since auxin retards the elongation of roots, a faster rate of elongation on the upper side is the result and this forces the root tip over until it is once more in the vertical position.

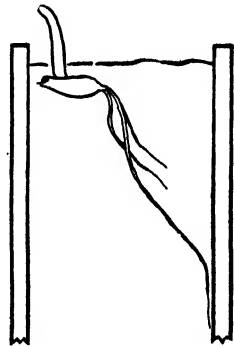


FIG. 190.—Oat seedling germinating in a glass-sided box illuminated from the left. The coleoptile is positively phototropic and the roots negatively phototropic.

**Phototropism.** Coleoptiles and most primary stems are positively phototropic, that is to say they curve towards a source of light. A few primary roots, such as those of cereals, are negatively phototropic (Fig. 190), but the great majority are insensitive to light and the direction of their growth is determined mainly by their positive

geotropism. Many leaves are diageotropic and their laminæ tend to take up a transverse position to the direction of the light falling upon them. The adjustment is most commonly carried out by unequal rates of growth in the petiole and the power of response becomes much less as the leaf ages. As a result the leaf becomes permanently fixed at a fairly early stage, and later light changes have no visible effect upon its position. The leaves of many plants do not exhibit adjustments of this kind at any stage.

The induction of phototropic stimuli in stems and coleoptiles, as well as in those roots that are sensitive, is limited to the growing tips, like that of geotropism. Decapitation leads to the same loss of power to respond. Coleoptiles capped with agar blocks containing auxin respond to light stimuli. If blocks are put on to one side, that side elongates more than the other. It appears, therefore, that phototropic curvatures are caused by a higher concentration of auxin in the side remote from the light; but how the redistribution is brought about by the light stimulus is still mysterious.

## Practical Work

### CORRELATION

(1) **Inhibition by the Dominant Bud.** Sow some broad beans in a five-inch flower pot. When the first leaf and the internode above have developed, cut off the tips from one or two plants. The buds in the axils of their first leaves will begin to grow; but will remain dormant in the undecapitated plants. If the new shoots are removed in their turn, the buds in the axils of the cotyledons will start to grow out.

(2) **Root-forming Hormones.** Make cuttings of catmint, wallflower or other convenient plants. Divide the cuttings into two lots. Stand one lot with the stems in about an inch of water and the other in an auxin solution overnight. Commercial preparations such as "Hortomone" are suitable. Then plant the cuttings firmly in wet sand and keep enclosed. After a week or a fortnight examine for root formation.

### IRRITABILITY

(3) **Phototaxis.** *Chlamydomonas* can usually be found in water butts during the summer months. Strain or filter off enough to colour a small beakerful of water perceptibly green. Cover with brown paper, including the top, but leave a slit at one side directed towards a bright window. Examine at the end of the day. The glass in the direction of the slit will be a bright green from the algæ gathered there, but the rest of the water will be colourless.

(4) **Geotropic Response.** Germinate broad beans in wet sawdust mixed with sand. Take beans with roots about an inch long and mark 2 mm. divisions from the tip backwards. Mark the divisions by drawing out a fine thread of enamel between two pins and then dropping it across the root. It will adhere when dry and not damage the root. Pass long pins through the beans and fix them to the cork of a wide-necked bottle with some water in the bottom. The roots must

be in a horizontal position. Next morning, measure the length of each division and notice that bending has occurred in the region of greatest elongation.

(5) **Phototropic Response.** Germinate about two dozen oat grains in a pot of damp soil kept strictly in the dark until the coleoptiles are about half an inch high. Cut off the top two millimetres from several plants in a red light such as a dark-room lamp. Cover the pot with a cardboard or black paper cylinder, closed at the top, but with a slit at one side. Illuminate by a 40-watt electric lamp placed about 1 foot from the slit. Turn out the light and examine the seedlings by red light after two and four hours. The uncut coleoptiles will have curved to the light, but not the others.

## Chapter XXII

### THE FLOWER

A flower is a shoot, or the termination of a shoot, that is specialised for reproduction. Its leaves are modified in various ways, some of them forming sporophylls comparable with the sporophylls of the cones of *Selaginella* and *Pinus*. In addition, it has further floral leaves that do not bear spores, but serve to protect the flower or to render it conspicuous. The production of a flower usually terminates the growth of its shoot; only rarely does the terminal bud survive to form new internodes and foliage leaves above the remains of the flower.

#### *Inflorescences*

Flowers are commonly produced in clusters or inflorescences, which are branching shoot systems. If the branching is monopodial, the flowers arise as side shoots each in the axil of a bract, the lowest maturing first. In this way a raceme (Fig. 191 A) is formed if the flowers are stalked, or a spike (Fig. 191 B) if the stalk is short or absent. A pendulous spike is a catkin such as is formed by hazel, alder (Fig. 191 C), oak and other trees. Inflorescences are often sympodial, that is to say the first flower formed is terminal and later flowers are produced on successive lateral branches. A cyme of this sort is formed by the meadow buttercup (*Ranunculus acris*); a dichasial cyme with opposite laterals is produced by the white campion, *Melandrium album* and sandwort (Fig. 192 B). The terminal inflorescence of horse-chestnut is racemose (monopodial) in its main axis, but the branches become cymose (sympodial). Numerous variations of these main types are given descriptive names in systematic botany.

The angiosperms have an alternation of generations like *Selaginella* and *Pinus*, but the gamete-forming, sexual generation is reduced and hidden away inside the dominant sporophyte. Its re-

duction has gone to such lengths that its existence was only discovered as the result of an outstanding piece of microscopic research published by Hofmeister in 1851.

The flower, like the cones of *Selaginella* and *Pinus*, is primarily a spore-producing organ and, again like them, it produces spores of

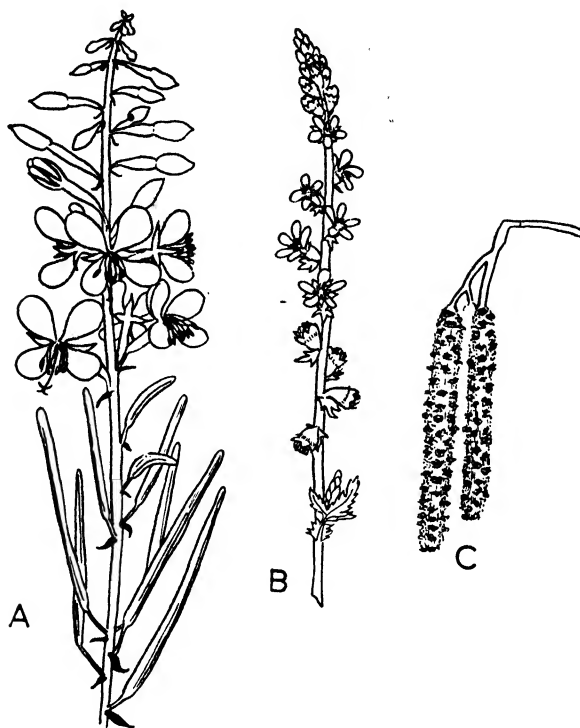


FIG. 191.—Racemose inflorescences. A, the raceme of *Epilobium angustifolium*. B, the spike of *Agrimonia eupatorium*. C, the catkin of *Alnus glutinosa*. All  $\times$  about  $\frac{1}{2}$ .

two different kinds, micro- and mega-. The microspores are in common language pollen, but the megaspores have no common name since they are hidden away inside. Pollen is transferred from one flower to another, and the formation of sperms and eggs can then go on inside one and the same flower, and fertilisation can take place without the need for any previous journey by swimming sperms. The enormous biological advantage this confers has resulted in the natural selection of plants which possess this curious and complicated mechanism, i.e. the angiosperms and gymnosperms, to



such an extent that they are just as dominant among plants as the mammals are among the animals.

### *Parts of the Flower*

There is almost endless variation in the structure of flowers which is related mainly to their methods of pollination and their ancestries. There are two principal agents in pollination—insects and wind. A single floral type of simple construction will be described to illustrate each of the two relationships.

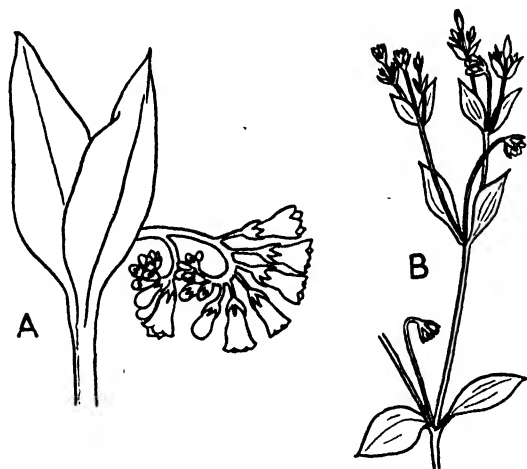


FIG. 192.—Cymose inflorescences. A, scorpioid cyme of *Symphytum officinale* with laterals all on one side.  $\times \frac{1}{2}$ . B, dichasial cyme of *Arenaria trinervis*. About nat. size.

### INSECT POLLINATION

*Ranunculus acris* L., the meadow buttercup, has a typical insect-pollinated flower producing both microspores and megaspores and eventually, therefore, both male and female gametes. It is of relatively simple construction that can be regarded as representing a prototype from which more complex constructions have been derived. Its axis, the receptacle—equivalent to the stem of a vegetative shoot—is much condensed so that the floral leaves are closely crowded together in whorls or close spirals.

### *Perianth*

The outer whorl of the perianth is formed of five sepals. In the bud they are green, hairy on the outside and entirely enclose the rest

of the flower. When the flower opens they become yellow and transparent at the edges. Collectively they are termed the calyx and provide an insulating and protective layer to the flower bud, comparable with the bracts of winter buds (cf. p. 261). In addition the perianth possesses an inner whorl, or corolla, of five petals alternating with the sepals (Fig. 193). They become much larger than the sepals and are bright yellow with a glossy sheen on their upper surface that

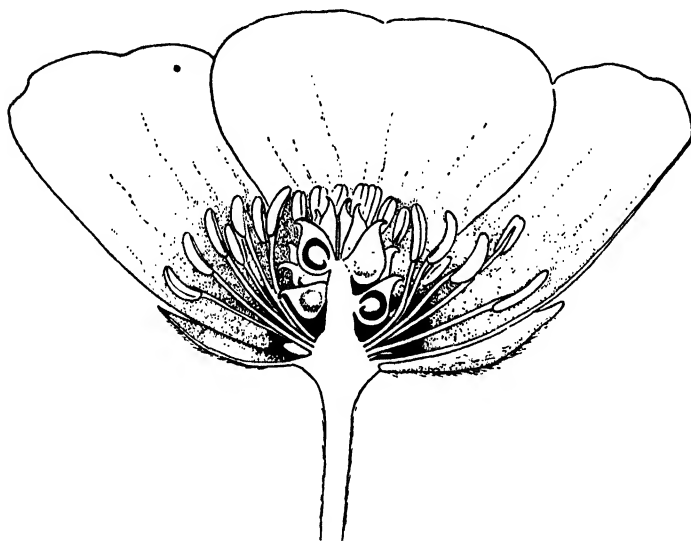


FIG. 193.—*Ranunculus acris*. Vertical section of the buttercup flower showing condensed stalk or receptacle at the centre terminating the peduncle and carrying the floral parts. From below upwards these are *sepals*, *petals*, *stamens* and *carpels*.  $\times 6$ . After James and Clapham.

makes them very attractive to the eye. At the base of each petal there is a small yellow flap attached only by its lower edge and below which is the nectary. This is the gland that secretes a sugary solution, the nectar, that attracts insects to the flower.

### *Andræcium*<sup>1</sup>

The sepals and petals are both sterile and never bear sporangia. The next set of floral leaves, the stamens, collectively the andræcium, bear microsporangia. They are very numerous—forty to seventy—and are inserted on a close spiral. They are much more highly

<sup>1</sup> Greek *ανδρος* (andros), a man, and *οικιον* (oikion), house, because the male gametes are formed by the microspores of the andræcium.

specialised and less leaf-like than the petals and sepals. Each stamen consists of a filament and a swelling at its upper end, the anther (Fig. 193). The essential parts of an anther are the four microsporangia (pollen sacs; Fig. 195), which are full of microspores (pollen grains) when ripe. The spores are shed through two long slits that appear on the outer faces of the anthers, each split throwing open the two microsporangia on one side of the anther simultaneously.

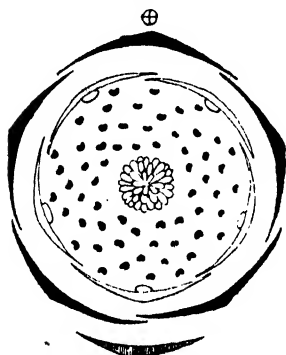


FIG. 194.—*Ranunculus acris*, floral diagram. This is a conventional plan of the flower to show the numerous spirally arranged carpels and stamens, the five overlapping petals with their nectaries (in white) and the five sepals (in black). The cross and circle sign indicates the position of the main stalk and opposite it is the bract in whose axil the flower is borne.

### Gynæcium<sup>1</sup>

Above the anthers is a spiral of about 30 carpels. Each carpel<sup>2</sup> is a separate organ and is not attached to any of the other carpels, as happens in more highly specialised flowers. Each is attached to the receptacle by a broad base and has a short projection at the upper end, the style, terminated by a narrow curved stigma (Fig. 193). The stigma is the organ that receives the pollen grains from other flowers and each carpel, below its stigma, forms a hollow chamber in which there is a single ovule.

### Pollination by Insects

Buttercups are pollinated by short-tongued insects, such as flies and bees.

When the flower opens all the stamens are curved upwards, completely covering the carpels. Those on the surface first begin to shed their pollen outwards and when their sacs are exhausted they curve downwards towards the petals. Others follow, the innermost dehiscing last. During this phase, small insects crawling about the flower in search of the nectar at the bottom of the petals become freely dusted with pollen, but do not come into contact with the stigmas, still hidden under immature anthers. When these have all ripened and curved back, insects coming from other flowers are likely to brush part of their pollen load on to the now exposed stigmas and so effect cross-pollination. Protandry,<sup>3</sup>

<sup>1</sup> Latin, women's apartments.

<sup>2</sup> Latin, carpellum, a little fruit, because the carpels later grow into fruits.

<sup>3</sup> Greek *πρωτος* (*prōtos*), first, and *ανδρος* (*andros*), man, because the pollen grains (from which the male elements develop) are ripened first.

in which the stamens ripen before the stigmas, is common among many sorts of flowers, especially those of simple construction, and

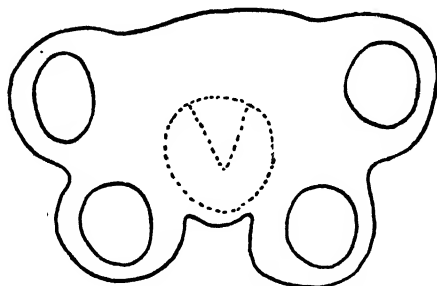


FIG. 195.—Diagram of a transverse section of an anther to show the arrangement of the four pollen sacs.

is often more complete than in buttercups. It increases the probability of cross-pollination in flowers whose structure would otherwise permit self-pollination to occur.

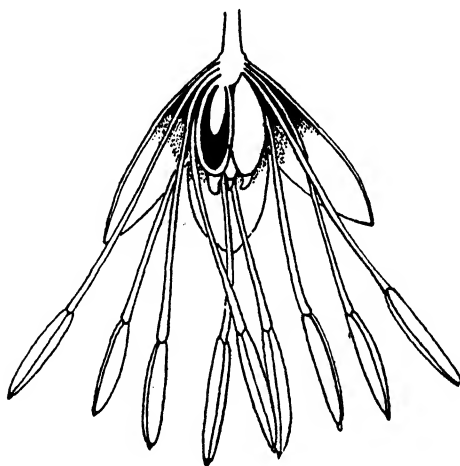


FIG. 196.—*Thalictrum minus*. Vertical section of the pendulous flower.  $\times 14$ . After James and Clapham.

#### WIND POLLINATION

*Thalictrum minus* L. The smaller meadow rue makes an interesting comparison with the buttercup. It belongs to the same family, *Ranunculacæe*, its flowers are constructed to the same general plan (Fig. 196) and are also borne in loose cymes. Nevertheless they are adapted to wind rather than to insect pollination.

*Perianth*

The perianth consists of a single whorl of five green sepals which are small and inconspicuous; there are no petals at all.

*Andræcium*

There are about twenty stamens inserted spirally above the sepals. They have long narrow anthers, and the filaments (stalks) are long, slender and flexible. They hang downwards, the whole flower being pendulous.

*Gynæcium*

The carpels are free, as in the buttercup, and each also contains a single ovule attached at its base (Fig. 196). The carpels are attached directly to the receptacle, as in the buttercup and, though they are longer, they have similar short styles with a stigmatic surface along the curved upper edges.

*Pollination by Wind*

In spite of its similar ground plan, this flower is much less attractive to insects than the buttercup. It is far less conspicuous, its small green sepals being no substitute for the buttercup's yellow petals.

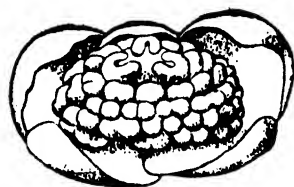


FIG. 197.—*Helleborus foetidus*, young flower showing the primordia of carpels at the apex and the numerous spirally arranged primordia of the stamens. Perianth segments are lower on the axis and already more fully developed. After Payer.

Furthermore, it has no nectary, so there is no honey to bring insects, and there is no easy foothold for them. On the other hand, it has several features that facilitate the distribution of its pollen by wind. The flowers are borne on long slender stalks and are easily shaken in the breeze, a feature which is repeated in the slender filaments of the stamens themselves. The anthers project clear away from the perianth, so there is no obstruction to the removal of the pollen. This is not a highly adapted wind flower, however, and the stigmas are small with correspondingly small likeli-

hood of receiving pollen grains. In more specialised flowers, like those of the grasses, the stigmas are large and feathery. Cross-fertilisation is favoured by the fact that the stigmas ripen before the anthers (protogyny), but later on both are functional together. Perhaps in this stage the fact that the stigmas are above the anthers

tends to restrict the chances of self-fertilisation. In more extreme types of wind-pollinated flowers, such as the catkins of oak and hazel, stigmas and anthers are produced on separate flowers in separate inflorescences, the pistillate and staminate catkins.

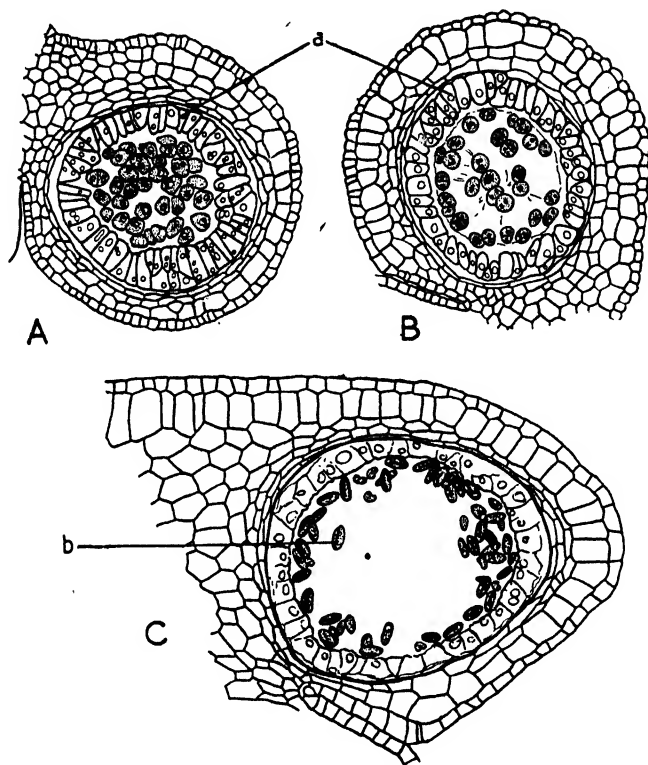


FIG. 198.—*Lilium candidum*. Transverse sections of parts of anthers showing the development of pollen grains in a single pollen sac. A, the sporogenous tissue in the centre has separated to form microspore (pollen) mother cells (shaded). Some of these have already begun the first division of meiosis. *a*, the tapetum. Outside this is the wall of the anther. The large cells below the epidermis become fibrous. B, formation of pollen tetrads. C, the pollen grains, *b*, have become separate and have developed thick outer walls. The tapetum has become exhausted, its material being consumed in the development of the pollen grains. The groove at the bottom is the point where adjacent pollen sacs break open together when the fibres below the epidermis contract.  $\times$  about 200.

#### DEVELOPMENT AND FERTILISATION

The spores and gametes of buttercups and meadow rue are small and difficult to examine. The cycle of development and fertilisation

is more conveniently followed in a larger flower, like that of the Madonna lily (*Lilium candidum*) which is described here.

### *Development of Pollen*

Each stamen arises as a papilla on the receptacle, just as a leaf arises on a vegetative apex (Fig. 197). Its swollen end develops into an anther with two lobes, one on each side of the stalk. Inside each lobe two long narrow tracts of tissue retain abundant protoplasm and divide actively. These are the microsporangia (pollen sacs) and

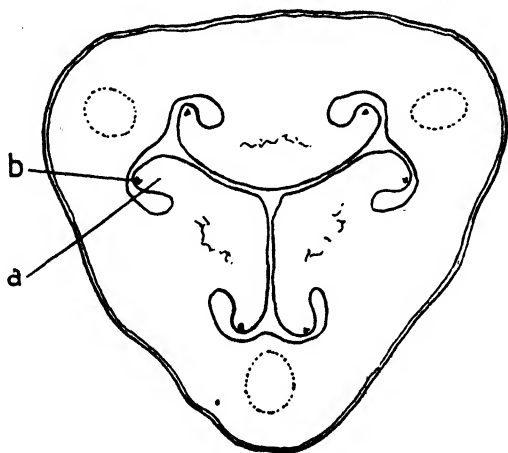


FIG. 199.—*Lilium candidum*. T.S. ovary of three fused carpels. *a*, nucellus; *b*, megaspore. The dotted circles show the midribs of the carpels.

all four of them run the full length of the anther. Eventually their cells round off from one another and become the spore mother cells (Fig. 198), each dividing into a tetrad of microspores. The double division of the spore mother cells is the reduction division or meiosis (see p. 149). The behaviour of the chromosomes at this important stage is described on page 332.

### *Development of the Ovule*

Ovules appear first as swellings upon the infolded edges of the carpels. Buttercups produce only one ovule in each carpel, but the lily has many. The first tissue to appear is called the nucellus (Figs. 199 and 200). It is a megasporangium and produces a single tetrad of megaspores just below its surface. Three of the four megaspores abort, leaving a single one to carry on. While this is happening,

two coats—an inner and an outer integument—grow up from the base of the nucellus and cover it over with the exception of a minute pore at the tip, the micropyle, which does not fuse up. The upper surface of the young ovule, to which the stalk is fused, grows more rapidly than the lower with the result that it curves round on itself until the micropyle faces the point of attachment to the carpel instead of being directly away from it (Fig. 201). This happens in the development of lilies and buttercups and perhaps in the majority of flowers, but not in all.

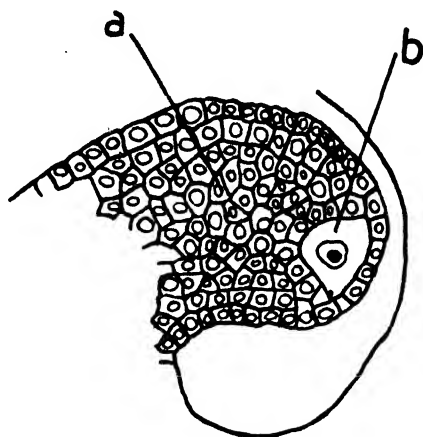


FIG. 200.—*Lilium candidum*. Median section of a young nucellus. *a*, general cells of the nucellus with conspicuous nuclei; *b*, megaspore.  $\times$  about 200.

### *Development of Gametes and Fertilisation*

The megaspore embedded in the nucellus performs three successive divisions without any corresponding formation of new walls. The cell enlarges greatly at the expense of the surrounding nucellus tissue, and at this stage is referred to as the embryo sac. It has eight nuclei consisting of two polar nuclei that have migrated to the centre (Fig. 201 E); three antipodals at the far end from the micropyle; and three nuclei clustered together at the micropylar end. Two of these are synergids<sup>1</sup> and the third is the egg. In the production of the egg no body is formed comparable to the archegonia of *Dryopteris*, *Selaginella* and *Pinus*, but the development of eight naked

<sup>1</sup> From Greek *σύν* (*sūn*), with; and *ἔργον* (*ergon*), work, i.e. "co-operate" from the notion that they may help to direct the pollen tube to the egg.



cells within the wall of the original cell is reminiscent of egg-formation in the oogonium of *Fucus*. In angiosperms, only one out of the eight becomes an egg, whereas in *Fucus* the number varies with the species.

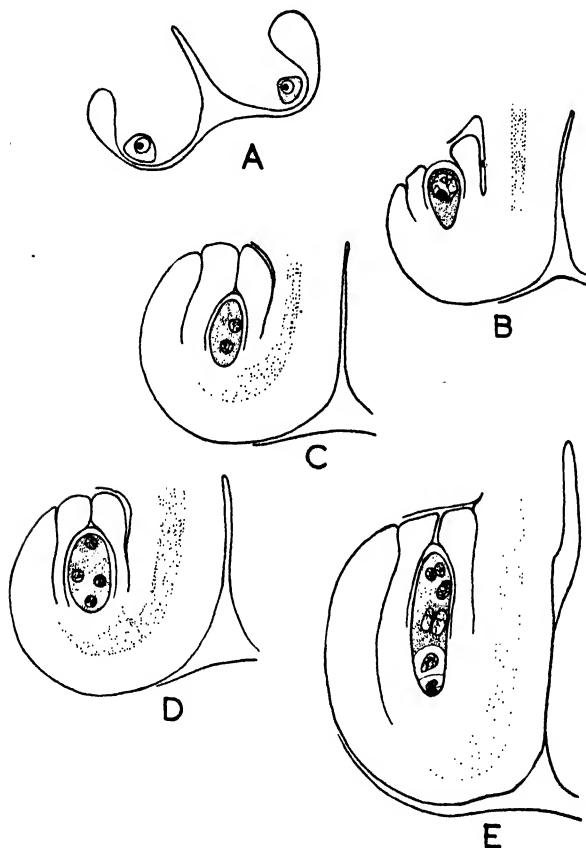


FIG. 201.—*Lilium candidum*, development of the ovule. A, young nucelli with megaspores. B, integuments forming; nucleus beginning meiotic division. C, binucleate stage. D, 4-nucleate stage. E, embryo sac complete, ovule ready for fertilisation.  $\times 160$ . After James and Clapham.

When the microspores are shed from the anthers they have already performed one division and have two nuclei. One is the grain or tube nucleus and the other, which has its own cytoplasm round it but no wall, forms the generative or sperm mother cell. The outer wall of the pollen grain is thickened and ornamented in a pattern character-

istic of the species (Fig. 202). When it comes into contact with a stigma (or with a simple sugar solution) the pollen grain germinates by putting out a tube through a thin place in the wall (Fig. 203).

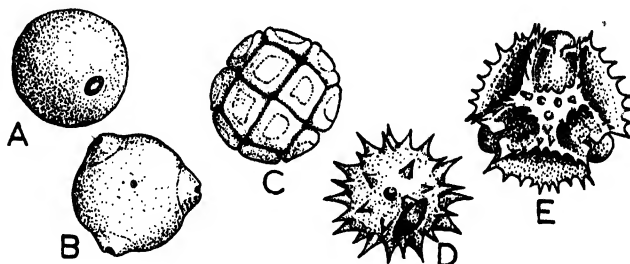


FIG. 202.—Pollen grains showing varying and characteristic sculpturings of the outer wall. A, *Phleum pratense*. B, *Betula populifolia*. C, *Acacia longifolia*. D, *Helianthus annuus*. E, *Taraxacum officinale*. Various magnifications between 500 and 750.

First the tube nucleus and then the sperm mother cell pass into the tube. It grows down through the loose tissue of the stigma and style; and, while this is happening, the sperm mother cell divides into two

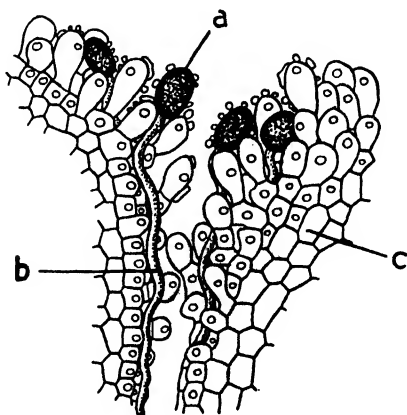


FIG. 203.—Pollen grains germinating in the stigma of a lily. a, pollen grain; b, pollen tube; c, stigma cells. Highly magnified. After Dodel-Port.

sperms (Fig. 204 C). The sperms have no flagella, though they are curved or spirally twisted like those of some of the lower plants. The growth of the tube conveys them passively to the embryo sac. When this is reached the soft end of the tube dissolves and the sperms are discharged into the embryo sac cavity. One of them then fuses

with the egg to produce the zygote, and the other forms a triple fusion nucleus by combining with the two polar nuclei. The usual time taken by the growth of the pollen tube is a few hours or days, and there is no dormant stage as with *Pinus*.

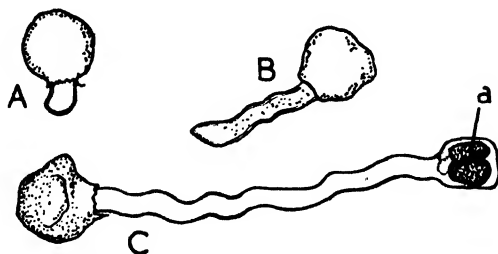


FIG. 204.—Pollen grains of a rhododendron germinating in a 5 per cent. sucrose solution. A and B, after 24 hours. C, after 44 hours; a, sperm nuclei.

The zygote grows into the embryo of the new plant and the triple fusion nucleus grows into a tissue known as the endosperm which, owing to its origin, has  $3n$  chromosomes in its cells. The embryo sac continues to enlarge at this stage by rapid vacuolation, and the

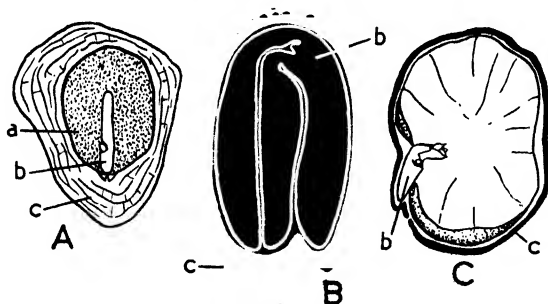


FIG. 205.—Seeds. A, *Lilium candidum*; a, endosperm; b, embryo with radicle, plumule, towards the left, and single cotyledon; c, winged testa.  $\times 3$ . After Scott. B, *Capsella bursa-pastoris*, shepherd's purse; b, embryo with radicle, two cotyledons and plumule showing between them; c, the testa.  $\times$  about 40. C, *Vicia faba*, broad bean; b, embryo with radicle and two large cotyledons, one removed to show the plumule; c, the testa. About nat. size.

endosperm is represented at first by wall-less cells round its edges. By degrees the cavity is filled, and walls are formed. The ripe lily seed contains an embryo embedded in endosperm. In some plants the growing embryo absorbs the endosperm which has totally disappeared by the time the seed is ripe (Fig. 205).

## Practical Work

### FLORAL STRUCTURE

(1) Cut a **buttercup flower** vertically through the centre with a razor or sharp scalpel. Draw the half flower on a large scale and label *receptacle*, *calyx*, *corolla*, *nectaries*, *stamens* and *carpels*. Make your drawing as exact and clear as possible without any loose ends (attachment of stamens, for example), and use no shading.

(2) Construct a **floral diagram** of the same flower and make sure that it checks with the longitudinal drawing. If buttercups are out of season, *Helleborus niger* (January), *Caltha palustris* (April), *Thalictrum aquilegifolium* (June), or *Clematis vitalba* (July and August) may be taken as variations on the theme.

(3) Make a similar study of *Thalictrum minus* or *Plantago major*. These are wind-pollinated flowers occasionally visited by insects.

### DEVELOPMENT AND FERTILISATION

(4) **Stamens.** Examine and draw with the help of your lens a complete stamen of *Lilium* (or tulip or fritillary) showing *filament*, *anther*, and *connective*, the continuation of the filament between the two halves of the anther. Cut a transverse section of a young anther. Mount in a drop of dilute glycerine and draw, showing the four *microsporangia* (pollen sacs), the *sporogenous cells*, the *vascular bundle* of the *connective*. Mark the *epidermis* and the *walls* of the *pollen sacs* below it.

(5) Examine a dehiscent anther similarly and note the method of opening.

(6) In prepared transverse sections of lily buds, look for stages of **microspore production**, including meiotic divisions of the microspore mother cells.

(7) **Carpels.** Examine the structure of a lily (or tulip) ovary. Note that it consists of three carpels with their edges infolded and bearing rows of ovules. Cut a transverse section, mount in dilute glycerine and make an outline diagram to show these arrangements.

(8) Examine prepared sections showing **ovules ripe for fertilisation**. Make a drawing showing the *integuments*, *micropyle*, *nucellus*, *embryo-sac* and the *vascular bundle* of the stalk. It is rarely that a single section shows all the eight nuclei of the embryo sac. (Why?) Examine several sections and construct a composite drawing showing the *egg*, *synergids*, *polar nuclei*, and *antipodals*.

(9) **Germinating Pollen Grains.** Soak small pieces of cellophane in water and dust with pollen from dehiscing anthers. Lay the cellophane on filter paper soaked with sugar solutions and enclose in Petri dishes to prevent drying up. The following may be used: tulip pollen with 20 per cent. sucrose; apple or pear pollen with 15 per cent. sucrose; *Tradescantia* pollen with 80 per cent. sucrose.

(10) Take any flower with small protruding **stigmas**. Cut them off, mount in dilute glycerine and examine under the microscope. Note the pollen grains adhering and look for germinating pollen tubes.

(11) Examine prepared slides of early and late stages of **embryo formation** in lily or shepherd's purse (*Capsella bursa-pastoris*).

## Chapter XXIII

### SEEDS AND FRUITS

When fertilisation has taken place the ovules begin to grow into seeds and the carpels into fruits. The changes involved are very considerable and very various in different species.

#### *The Seed*

The ripe seed of a lily contains three main portions, the embryo, the endosperm and the testa (Fig. 205 A). Since the lily belongs to the monocotyledons, its embryo has a single cotyledon and, at the opposite end, an embryonic root, the radicle, pointing towards the micropyle. The stem apex (plumule) lies in a notch opening at the side. The embryo is about half as long as the seed and is embedded in a massive endosperm, which occupies all the rest of the interior. The nucellus has by this time been completely absorbed and no trace of it remains. In some seeds, like castor-oil seeds, a thin papery layer surrounds the endosperm. It is called the perisperm and is the remains of the nucellus. The testa is derived from the two integuments and is flattened out into a papery wing surrounding the whole of the seed, which is the shape of a flat disc.

Buttercup seeds also have an embryo embedded in a relatively large bulk of endosperm. The embryo has two cotyledons, but is too minute for convenient examination. Shepherd's purse has seeds which when ripe are almost wholly occupied by the embryo. The radicle points, as usual, towards the micropyle, and the two large cotyledons are bent round to lie alongside (Fig. 205 B). Between the two cotyledons is the growing point of the embryonic stem. The testa is quite thin and but little developed from the integuments; the endosperm and the nucellus have both been completely absorbed by the embryo.

The cotyledon and radicles of the shepherd's-purse seed are of more or less equal sizes. In many seeds, where the embryo has

totally absorbed the endosperm, the cotyledons have become swollen to a much greater bulk than the radicle, and present the typical appearance of storage tissues. In broad beans (Fig. 205 C) they contain abundant starch.

The following are the corresponding structures in ovules and seeds. The *ovule* becomes the *seed*; the *integuments* become the *testa*; the *nucellus* becomes the *perisperm*, if it survives. The *triple fusion nucleus* develops into the *endosperm*; the *zygote* becomes the *embryo*.

### *Development of the Fruit*

The structure of a fruit depends both on the kind of gynæcium it has developed from and the method of its development. While the ovules are ripening into seeds, the rest of the flower is also undergoing many changes. The petals and stamens usually wither and fall off, but the calyx is most frequently persistent and sometimes goes on growing. The stigma and style dry up or are shed, but the parts of the carpel forming the walls of the ovary develop into the pericarp which is the wall of the fruit. The pericarp differs very much in different species. In buttercups it is thin and dry; in nuts thick and woody; in tomatoes soft and succulent.

### *Dry Indehiscent Fruits*

The single, unfused carpels of buttercups each contain a single ovule (Fig. 193). They grow only slightly after fertilisation and become brown and membranous as they dry up. Each contains a single seed, the product of its ovule. When ripe they are easily parted from the receptacle and shaken off by any slight jar. Lying on moist soil, the pericarp slowly softens and decays and, when the seed inside germinates, it easily pushes out its radicle through the remains. Such a fruit, having no special opening mechanism, is termed indehiscent.<sup>1</sup> All the buttercups and many of their allies, roses and numerous other plants have one-seeded fruits of this kind, distinguished under the name of *achenes*. If the pericarp becomes hard and woody, the result is called a *nut*.

### *Dehiscent Fruits*

Dry fruits that contain numerous seeds are almost always dehiscent, i.e. they open by predetermined slits or pores, that facilitate the distribution of the seed. A pea or bean pod is a simple dehiscent fruit developed from a single carpel and containing a row of seeds.

<sup>1</sup> Latin, *dehisco*, gape, split open, with negative prefix *in-*.

It splits open along both sutures, representing the edges of the carpel to which the ovules were attached and the midrib. The sudden splitting of broom (*Sarothamnus scoparius*) pods, due to the tension of the drying walls (Fig. 206 B) throws the seeds out to some distance. Monocarpellary fruits, splitting down both sutures, are distinguished by the name of *legumes*; those which split along one suture only are called *follicles* and are common in such members of the *Ranunculaceæ* as *Caltha*, *Helleborus*, columbines and larkspurs (Fig. 206 A).

Most dehiscent fruits are *capsules*, formed\* from syncarpous gynæcia in which the carpels were joined together, instead of being

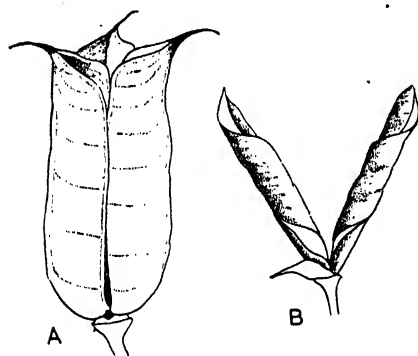


FIG. 206.—A, follicles of *Delphinium*.  $\times 5/3$ . B, Legume of *Sarothamnus scoparius*, broom. Nat. size. Both dehiscent.

free from one another as in buttercup and the othertypes described above. Capsules are of very various forms, being derived from gynæcia with different numbers of carpels, and they dehisce in a great variety of ways. The lily has a capsule (Fig. 207 A) that opens by three longitudinal splits corresponding with the midribs of the carpels. The disc-shaped seeds are arranged in six rows, two in each compartment,

like stacks of coins, and are easily jarred out of the open capsule. Two more of the many kinds of capsules are shown in Fig. 207.

### Succulent Fruits

During the development of succulent fruits, the carpels grow enormously and form a soft and juicy pericarp whose outer layer is a tougher skin. The cavities of the ovary may become obliterated during this growth, so that the seeds are embedded in juice or a pulp of large, thin-walled cells. The simplest succulent fruit is the *berry* (Fig. 212 A and B). Wild arum (*Arum maculatum*) fruits, tomatoes and oranges are good examples. The *drupe* is a succulent fruit derived from a single carpel which, besides a succulent layer, has developed a hard stony layer inside it. The "stone fruits," cherries, plums (Fig. 208 A), apricots and peaches are of this type.

Inside the stone the kernel consists of a single seed with a papery brown testa and two large, white cotyledons familiar in the form of almonds.

In the examples just quoted, the pericarp is developed from the carpels alone. In many of the more highly developed flowers in which the ovaries are sunk into the receptacle, the receptacle and the carpels are fused together. The pericarps of their fruits, therefore, have a dual origin. This applies, for example, to gooseberries, currants and honeysuckle berries. In apples and kindred fruits, collectively called *pomes* (Fig. 208 B), the receptacle is fused with the

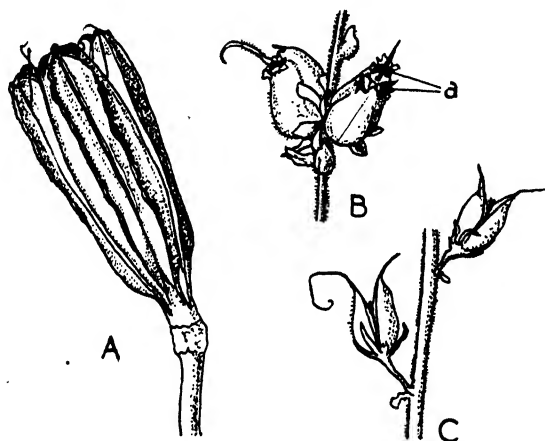


FIG. 207.—Capsules. A, capsule of lily. B, *Antirrhinum majus*; a, pores. C, *Penstemon*. All  $\times 2/3$ .

walls of the five carpels, themselves separate from one another. Both receptacle and ovaries increase greatly in size, the ovaries forming the tough core and the receptacle the continuous fleshy mass embedding them. The ovaries remain separate from one another—as can be seen by cutting a cross-section—and are in communication with the outer air at the apical end opposite the stalk.

### *False Fruits*

There are many fleshy structures associated with seeds which are not pericarps, being derived from sources other than the carpel. For instance, a pineapple is an entire inflorescence in which perianth, stamens, bracts and axis all become fleshy. A strawberry consists of



a fleshy receptacle which enlarges after fertilisation, bearing numerous achenes, themselves fruits, upon its surface. Rose hips are fleshy receptacles that have grown up to enclose their achenes in an urn (Fig. 209 E and F). Mulberries (*Morus* spp.) are formed from an inflorescence of several flowers in which the perianth leaves become succulent and enclose the pip-like ovaries (Fig. 209 A and B). Such examples could be multiplied almost indefinitely.

#### DISPERSAL

Seeds are the principal means by which plant species are spread over the face of the earth and there are three main agencies by which

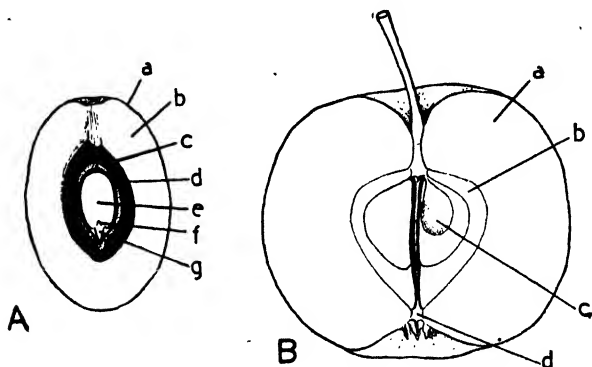


FIG. 208.—Succulent fruits. A, plum; a, epicarp (skin); b, mesocarp (flesh); c, endocarp (stone); d, testa; e, cotyledon; f, plumule; g, radicle. B, apple; a, flesh derived from the receptacle; b, core derived from the carpels; c, seed; d, open pore where receptacle has not fused over the carpels. Remains of the sepals are seen round the opening.  $\times \frac{1}{2}$ . After James and Clapham.

it is done ; animals, wind and water. Seeds may be distributed individually or while still within the fruit.

#### Dispersal by Wind

Wind is an important agent in dispersing seeds and fruits that are not too big, and that have a large ratio of surface to bulk. The flattened, almost paper-thin seeds of lilies are obviously adapted to wind dispersal. The seeds of the willow herb (*Epilobium* spp.) are plumed with tufts of fine hairs, and float away in the wind as they are released from their capsules. The seeds of *Pinus* (cf. Fig. 210 D) also have wings.

Winged fruits are commoner than winged seeds. Sycamore fruits (Fig. 211 B) are a well-known example. There are two joined carpels

in the flower and from the side of each a wing grows out as the pericarp ripens. The fruit spins as it falls, and the delay this entails increases the time for dispersal. The single-seeded fruits of ash (Fig.

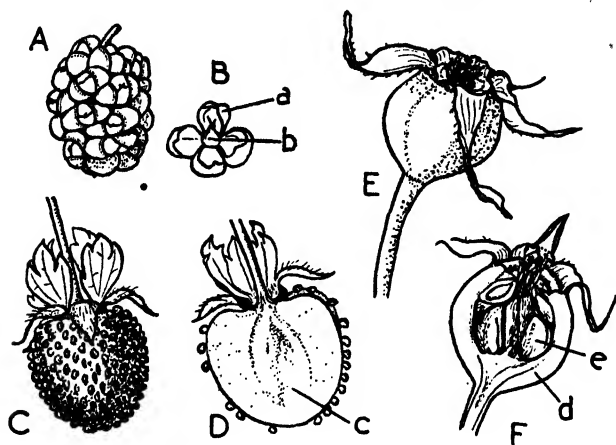


FIG. 209.—False fruits. A, mulberry, an inflorescence with fleshy perianths. B, single mulberry flower; *a*, fleshy perianth segment; *b*, ovary which forms a pip. C, strawberry, a fleshy receptacle with dry pippy fruits. D, the same in vertical section; *c*, the flesh of the receptacle. E, a rose hip, a fleshy receptacle enclosing a group of achenes. F, the same in longitudinal section; *d*, fleshy receptacle; *e*, achenes with persistent dried styles protruding from the top of the urn. All about nat. size.

211 A), birch and hornbeam are similarly assisted. In the last two the wings are formed by adherent bracts, not from the pericarp.

Other features that increase the wind surface of some fruits are

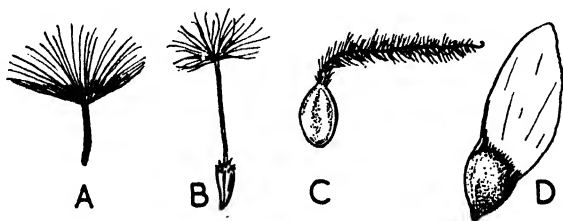


FIG. 210.—Wind-dispersed fruits of A, *Aster cordifolius*; B, dandelion and C, *Clematis recta*. D, seed of *Pseudotsuga*, a gymnosperm. All  $\times 2$ .

plumes and hairs of various kinds. Old man's beard (*Clematis vitalba*) has achenes with long persistent styles from which grow numerous hairs. The fruits of the Composite family commonly have a pappus of hairs derived from the calyx, attached either directly to

the top or on a stalk (Fig. 210 A and B). These fruits make very efficient parachutes and may be carried long distances on an up-draught.

### *Dispersal by Animals*

Some indehiscent fruits have hooks which catch on the fur of passing animals or on the clothes of passing men and so achieve a wide dispersal. The pericarp of cleavers (*Galium aparine*) is furnished in this way (Fig. 212 E and F) and the style of herb bennet (*Geum urbanum*) persists to become a single hook (Fig. 212 C and D).

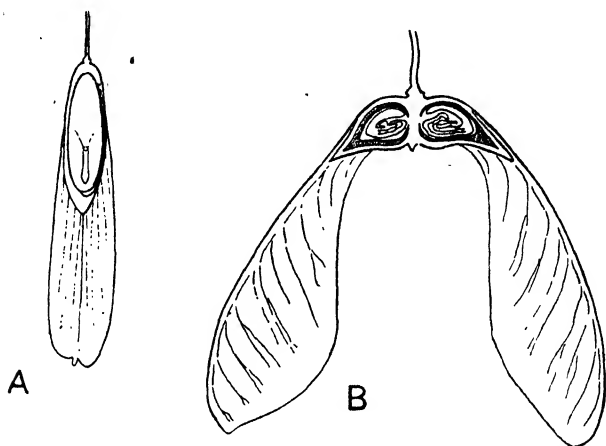


FIG. 211.—Winged fruits of A, ash and B, sycamore. After James and Clapham.

Animals constantly distribute small dry seeds and fruits with no special modifications except their smallness, by carrying them about in crevices of their bodies and in mud adhering to their feet and legs. It is instructive to examine a bird-bath after a few birds have dabbled in it, and even more so to examine the turn-ups of one's trousers after a walk through a wood or meadow. An almost incredible number of different seeds and small fruits may be found adhering to the boots and clothes of those who spend much time in the open country.

Succulent fruits are sought and eaten eagerly by birds and ground animals. The seeds, covered by the hard inner layers of pericarps or hard testas, pass through the alimentary tract unharmed, and are deposited often at great distances. *Atropa belladonna*, which has large black berries (Fig. 212 A), is soon spread by birds over wide

areas round fields into which it is introduced. Succulent fruits are not always successfully eaten by the distributing agent. Mistletoe berries have a very sticky pulp, and birds that peck at the fruit afterwards try to rub it off their beaks against the side of twigs. The seeds germinate in the crevices of the bark where they stick, and the haustorial roots of the seedling penetrate into the wood.

### *Dispersal by Water Carriage*

Seeds or fruits that drop into water and float may be carried considerable distances by river. Many seeds soon become waterlogged

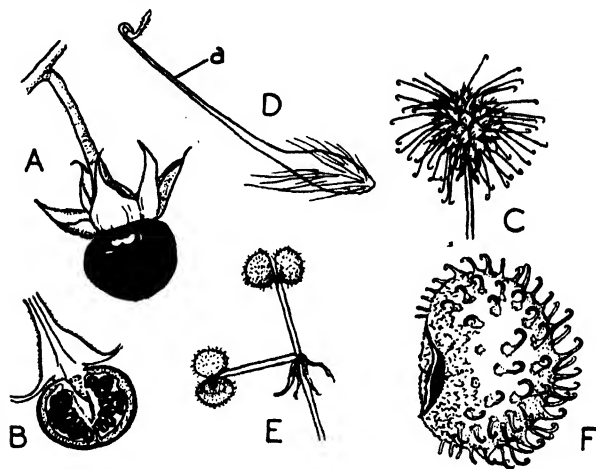


FIG. 212.—Fruits dispersed by animals. A and B, berries of *Atropa belladonna*.  $\times 2/3$ . C, achenes of *Geum urbanum* about nat. size. D, a single achene; a, the persistent hooked style.  $\times 4$ . E, the schizocarp of *Galium aparine* about nat. size. F, a partial fruit showing the hooks on the pericarp.  $\times 5$ .

and sink, but others may float for weeks or months. A piece of waste land beside the Thames near Oxford has been colonised by seeds of exotic plants washed down from the Botanic Garden a mile or so upstream. They include species like thornapple (*Datura stramonium*), not specially adapted for water or other carriage. Newly formed islands of coral or volcanic origin are supposed to be plant-populated by sea-borne fruits. The coconut is the best known example, the very thick, loose-fibrous pericarp being very light and not easily waterlogged. The life of the embryo is not very long, however, and those which come ashore after long periods of flotation are no longer viable.

## Practical Work

### STRUCTURE OF THE SEED

(1) Take a capsule of shepherd's purse that is fully grown but still green. Pull off one side and transfer the exposed seeds to a microscope slide. Break the testa of one or more with a pair of mounted needles. Cover with a drop of dilute glycerine and a coverslip. Examine under the low power. Note the thin-walled *testa* with chloroplasts in some of its cells and the shadowy *embryo* within. Press very gently on the coverslip till the embryo is squeezed out of the ruptured testa. Note the *radicle*, green *hypocotyl*, two *cotyledons* with *apical bud* between them. Other types of seed are examined in Exp. (1-9), p. 322.

### STRUCTURE OF FRUITS

(2) **Dry Indehiscent Fruits.** Examine and draw the following fruits: *Achenes* of buttercup, *Clematis vitalba*, ash, herb-bennet. Also fruits of sycamore and dandelion, or other Composite.

(3) **Dry Dehiscent Fruits.** Draw the following: *legume* of pea, sweet pea or bean. *Follicle* of *Caltha* or *Delphinium*. *Capsules* of lily, iris, poppy, *Antirrhinum*, campion or similar examples.

(4) **Succulent Fruits.** Draw a cherry or plum. Cut it in half longitudinally; get the stone out and break it open. Construct a sectional drawing of the fruit.

(5) Draw a **tomato** or **gooseberry** and then make transverse and vertical sections. Make drawings to show the parts of the *pericarp*—*pulp* and *juice*—and the arrangement of the seeds.

(6) Draw transverse and median-longitudinal sections of an **apple** to show the construction of the *pericarp* and *core*. If young stages are available, comparative drawings should also be made.

## Chapter XXIV

# GERMINATION

### *Dormancy and Viability*

Ripe seeds in the condition described in the last chapter are usually ready to germinate when brought under suitable conditions. Some few, like apple and juniper, need a period of after-ripening during which invisible changes are running to completion. A ripe seed awaits germination in a condition of dormancy. It is "dry," i.e. has about 15–20 per cent. moisture instead of the 80–90 per cent. present in active tissues, and is more or less isolated from its surroundings by its testa and by the pericarp if still within the fruit. Growth is at a standstill and respiration goes on with exceeding slowness. The wet dormancy experienced by the seeds of bog plants and others is slightly different. The seed has a high water content but is narcotised by a low pressure of oxygen and a high one of carbon dioxide.

Seeds may survive a long time under very unfavourable conditions while dormant and dry. They will survive extreme cold,  $-250^{\circ}\text{C}$ . has been tried, and seeds up to about 200 years old have been known to germinate. The alleged germination of wheat from Egyptian and Aztec tombs and from the granaries of Herculaneum is apochryphal. Wheat grains die within ten years and some seeds much sooner. As gardeners know, parsnip seed has to be sown within its first season and many seeds germinate much more freely if the dormant period is curtailed or avoided. Few seeds are worth much after ten years of ordinary storage.

### *Conditions for Germination*

The first requisite is *liquid water* and often the mere addition of water is enough to start germination. The sprouting of oat grains during a wet harvest is a familiar and tiresome example. A few ripe seeds, like acorns, may even contain enough water to germinate at

once if evaporation is checked by keeping them in a moist atmosphere. Once they have lost a certain proportion of their water they must, like other seeds, have more supplied from outside before they will germinate.

The second requisite is *free oxygen*. The living cells of the embryo must be able to respire aerobically; anaerobic respiration—with rare exceptions such as rice grains—is unable to promote germination.

The third requisite is a *suitable temperature*.

Protoplasm is inactive at temperatures near  $0^{\circ}\text{C}$ ., and no germination occurs even if water and oxygen are supplied. Above zero the chemical changes on which germination depends take place with increasing rapidity as temperature rises, and germination is accelerated accordingly. Above  $30\text{--}40^{\circ}\text{C}$ ., depending upon species, the working of the protoplasmic system begins to break down owing to coagulation and probably other causes, and the young seedling is killed.



FIG. 213.—Corroded starch grains from the endosperm of germinating barley. A hollow pellicle remains undigested.  $\times$  about 350.

#### *Enzyme Formation and Activity*

As soon as germination starts, rapid metabolic activity sets in, catalysed by the enzymes of the embryo. Some of these are preformed in the dormant embryo, having been manufactured during its maturation. The carboxylase (see p. 83) of barley grains belongs to this group. Others, like the invertase of barley grains, arise rapidly as germination proceeds.

The embryo itself has only a priming of reserve food, its cells being full of active protoplasm. As soon as germination is actively in progress the reserves in the endosperm, or in the swollen cotyledons if the reserves have been transferred before dormancy, are digested and moved to the growing points. Starch is acted upon by amylases (Fig. 213), fats by lipases, reserve proteins by the proteases. The large quantities of sugars released are used in the co-ordinate reactions of growth and respiration; new cell walls are formed, vacuoles begin to swell as sugar solutions accumulate, and rapidly increasing quantities of carbon dioxide and heat are liberated. The proteins, broken down to amino-acids and amides in the reserve tissues, are reassembled as different, protoplasmic proteins in the growing points (Fig. 214).

### *Rupture of the Seed Coat*

As water is taken up the seed swells and becomes turgid. The seed coat is not broken at this stage, being sufficiently elastic to take up the swelling. It may even stretch more than the internal tissues; the seed coats of French and runner beans (*Phaseolus*) wrinkle up into ridges when the beans are soaked. The growth of the young embryo soon exceeds the capacity of the testa for stretching, and the young radicle breaks its way out, often at or near the site of the micropyle. The resistance of seed coats to rupture usually falls very much on wetting. Thus, a hazel nut testa with a breaking strain of about 120 lb. to the square inch when dry has been found to break at about 45 lb. to the square inch when soaked. Some very resistant walls, like those of castor-oil beans and *Canna*, called Indian shot, hold up germination until they have rotted away.

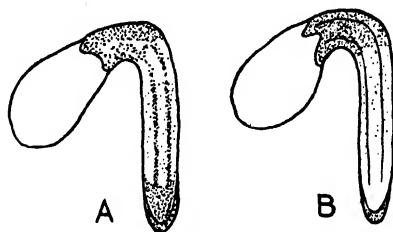


FIG. 214.—Diagrams of potato seedlings showing the distribution of the principal substances. A, protein, abundant in meristem, procambial strands and hypocotyl. B, starch, in root-cap and hypocotyl. The white area in the elongation zone contains abundant sugars. After Penston.

### *Structural Changes During Germination*

The first visible change is always the pushing-out of the radicle as it ruptures the testa. Being positively geotropic it turns downwards into the soil, becoming the main tap-root and often grows to surprising lengths before the shoot appears. In monocotyledons and other plants with fibrous root systems, the development of the radicle stops at an early stage and other roots grow from the base of the stem.

In following the development of the shoot, two types have to be distinguished. In what is by far the commonest, the hypocotyl elongates enormously and carries the cotyledons out of the soil and up into the air. This happens when the root has already become well anchored in the soil. The elongation of the hypocotyl either hauls the cotyledons out of the testa or carries it aloft still adhering to the



cotyledons until it is finally shed. As soon as the cotyledons come above ground the curve of the hypocotyl (Fig. 215) straightens out, and the cotyledons become green and horizontal. The straightening of the hypocotyl is a response to light. This type of germination is called *epigeal*,<sup>1</sup> making reference to the cotyledons coming to the surface. Good examples are provided by the endospermic seeds of the castor-oil plant and the non-endospermic seeds of marrow and

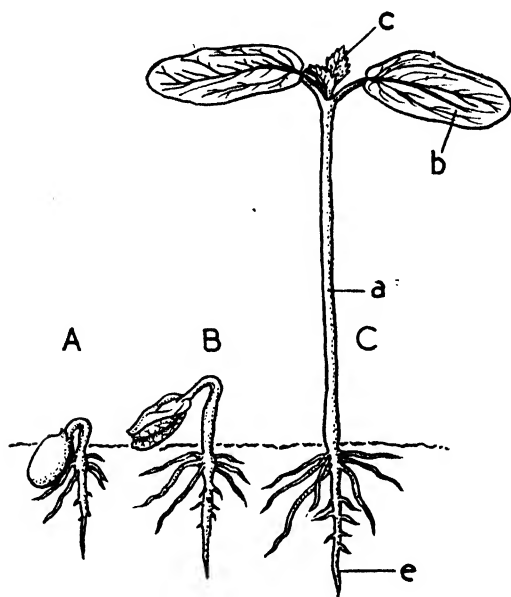


FIG. 215.—A–C, stages in the germination of castor oil, an endospermic seed with epigeal cotyledons. *a*, hypocotyl; *b*, cotyledon; *c*, epicotyl; *e*, radicle.  $\times$  about  $\frac{1}{2}$ . After Nelson.

runner beans. Marrows are notable for developing a peg of tissue from the base of the hypocotyl, which holds down the lower side of the testa. The seed is flat, and the two valves of the testa enclose the cotyledons rather like the two valves of an oyster shell. The growth from the lower side of the hypocotyl fixes the lower side of the testa in position while the cotyledons are dragged out by the growth of the upper part of the hypocotyl. This is a very specialised arrangement without parallel in other seeds, in which (very rarely) germination can be seen to fail because the cotyledons and the stem apex cannot get rid of the old testa.

<sup>1</sup> Greek *ἐπί* (epi), upon; and *γῆ* (gē), earth.

The second type of germination is called *hypogeal*<sup>1</sup> because the cotyledons remain within the seed coat underground. The hypocotyl does not elongate, but the bud between the cotyledons begins to grow directly the root has well established itself. It develops with the elongating zone making a sharp curve (Fig. 216) and the actual apex hanging downwards. Like the curvature of the hypocotyl in epigeal germinations, this is caused by the absence of light and it straightens

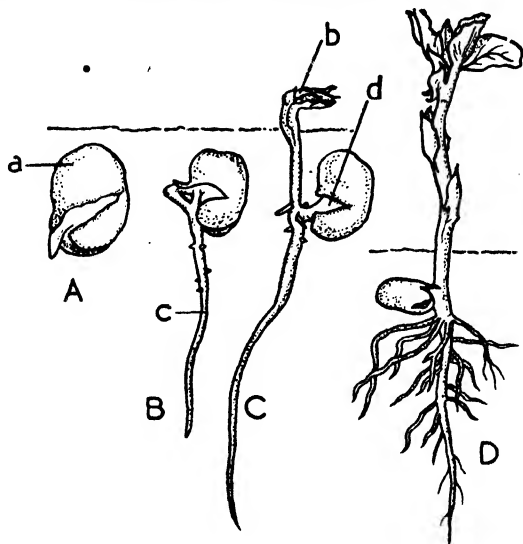


FIG. 216.—A-D, stages in the germination of broad bean, a non-endospermic seed with hypogeal cotyledons; *a*, testa; *b*, epicotyl; *c*, radicle; *d*, cotyledon.  $\times$  about 2/3. A-C after Priestley and Scott. D after Nelson.

out as soon as the apex comes above ground (Exp. (7), p. 322). Hypogeal germination is much less common than epigeal, but is familiar in peas and broad beans.

A somewhat specialised but highly important group, the cereals and grasses, also have hypogeal germination. The cereal grains and grass "seeds" are really fruits, achenes, in which the pericarp and testa have become fused into a single coat. Further specialisations are that the single cotyledon has become the scutellum<sup>2</sup> and the first foliage leaf has become a permanently rolled tube without chlorophyll, the coleoptile<sup>3</sup> (Fig. 217). The scutellum faces the endo-

<sup>1</sup> Greek *ὑπό* (hupo), below.

<sup>2</sup> Latin, little shield, from its shape in surface view.

<sup>3</sup> Greek *κολέιον* (koleon), a sheath; and *πτίλον* (ptilon), a wing, as a thing that protects.

sperm and secretes enzymes into it that hydrolyse its cellulose and starch. The scutellum remains an organ of the seed, and absorbs the hydrolysed reserves into the embryo. After a cluster of roots has been established the coleoptile breaks out of the grain and comes to the surface, the growing point being concealed and still underground

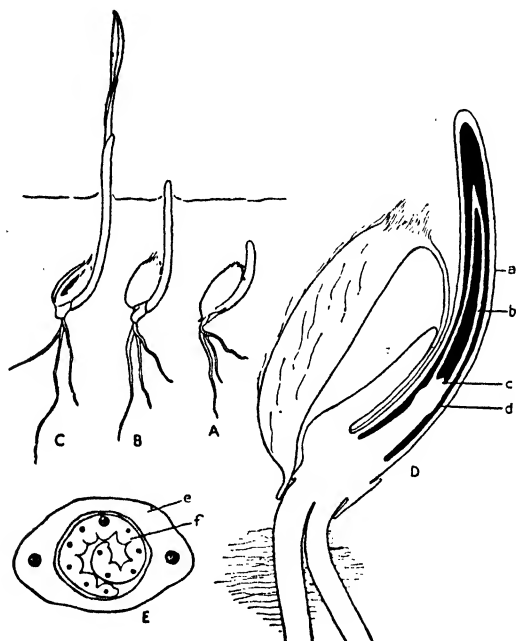


FIG. 217.—A–C, stages in the germination of a wheat grain with endosperm and hypogeal cotyledon. D, as B, enlarged; *a*, coleoptile; *b*, first foliage leaf; *c*, stem apex; *d*, node. E, transverse section of coleoptile, *e*, showing the first leaf, *f*, rolled inside it.

within it. The first foliage leaf grows out through a pore at the tip of the coleoptile and then unrolls and turns green (Fig. 217 C).

### *Use of Seeds by Man*

Seeds always contain reserve tissues in which valuable foods, carbohydrates, fats and proteins are stored. These reserves, like those of fleshy roots (p. 179), are turned to human account. The cereal grains—wheat, barley and rye—provide the fundamental food of the temperate zones, and rice that of the oriental tropics. Maize and oats are important both as human and as stock food. The legumes—peas, beans, soya and lentils—are second in importance

only to the cereals. All these seeds are cultivated for their stocks of starch. They also contain proteins, relatively little in rice, more in wheat and most in soya, the "beef-steak plant."

The fat-containing seeds are extracted, not ground like the starch-containing ones. Chief of these are the palms of West Africa (*Elais guinéensis*) and of the South Seas (*Cocos nucifera*), which are the source of the margarine fats. Other important food oils are cotton-seed oils used for food as well as for technical purposes; olive oil, the historic food-oil of the Mediterranean basin, and ground nuts (*Arachis hypogaea*) now in process of wide development.

### *Death Rate and Competition*

The germinating seed and the young seedling are the most vulnerable stages in the life of a plant. The death rate under natural conditions is enormous. Many seeds fall in places where they cannot successfully germinate and many are eaten by birds. Many seeds that do begin to germinate are killed at an early stage by lack of soil in which they can root, of light and air-space in which they can spread their shoots, or by attacks of fungi and insects. As soon as they get a little larger they are liable to be eaten off by rodents or browsing animals. No seedling of a woody plant can survive, for example, in a heavily grazed grassland. Perennial herbaceous plants, like the grasses, survive on such land, because of their surface and underground shoot systems, which possess buds that grow out when the upper parts are eaten off.

Many plants, especially those like foxgloves, poppies and mulleins that form minute seeds in capsules, produce them in enormous numbers: a single plant may scatter more than a hundred thousand. If only ten of these survived and the process were repeated by the progeny for twelve years, a population of a billion ( $10^{12}$ ) would arise from a single plant; enough foxgloves to cover about 35,000 square miles to the exclusion of all other plants. Many species are actively spreading and increasing their territory at the present time, though at nothing like such a rate as that. Others are decreasing, like the Bristol rock cress (*Arabis stricta*) in this country at least, where it is failing to maintain itself in the struggle for light, air and water. Probably the majority of species are more or less holding their own, and it is mainly by *competition* between individuals of the same and different species that this fluctuating balance is established and maintained and the spread of any one species limited. The balance arrived at in any particular locality is exceedingly complicated and

delicate. The introduction of a new factor, such as drier soil due to draining, may have far-reaching and unpredictable results. A new species coming in from outside may come to dominate the area like the prickly pear cactus (*Opuntia* spp.) introduced into Australia; or it may disappear entirely, or may settle down as an established component of the equilibrium, like the South African figwort (*Mesembryanthemum*) on the cliffs of Cornwall.

### Practical Work

#### A. CASTOR-OIL PLANT: A SEED WITH OILY ENDOSPERM AND EPIGEAL COTYLEDONS

(1) Remove the brittle *testa* from a seed. Note the papery *perisperm* surrounding the oily *endosperm*. Split this open carefully along the narrow edges. The thin *cotyledons* with well-marked veins will be found in the centre, extending almost the full length of the seed. Note the *radicle*, *hypocotyl* and *apical bud* between the *cotyledons*.

(2) Draw a series of germination stages showing the growth of the *radicle* into a tap-root and the elongation of the *hypocotyl* bringing the *cotyledons* above ground. Note the buds in the axils of the *cotyledons*.

#### B. VEGETABLE MARROW: A SEED WITH PERISPERM AND THICK EPIGEAL COTYLEDONS

(3) Note the flattened form of the seed, the *scar* of attachment to the fruit wall and the nearby *micropyle*. Split the seed lengthwise and observe the greenish *perisperm*, two rather thick *cotyledons* and the *radicle*.

(4) Make drawings of a series of germination stages showing the development of the root and of the peg on the *hypocotyl*, the opening and straightening of the *hypocotyl*, and the greening of the *cotyledons*.

#### C. BROAD BEAN: A SEED WITHOUT ENDOSPERM AND WITH HYPOGAEAL COTYLEDONS

(5) Make drawings of the front and side views of the seed, showing the *scar* of attachment and the *micropyle* at one end of the *scar*. By squeezing a soaked bean, water will be forced out through the *micropyle*. Remove the *testa* and show the two massive *cotyledons*, the *radicle* and the *apical bud* above the *cotyledons*.

(6) Draw germination stages marking *cotyledons*, *foliage leaves*, *young stem*, *axillary buds*, *terminal bud*, *primary root* and *lateral root*. The *hypocotyl* remains short.

(7) Plant two or three peas near the bottom and against the side of a glass-sided box. Fill with fine soil, and water. Set up a second box in the same way. Keep one in a bright light and the other in the dark. The shoots of the peas in the dark will remain curved and will get above ground without difficulty: those in the light will straighten out while still underground.

(8) Weigh six dry beans and six after soaking and gently drying the surface. By what percentage does their weight increase?

D. WHEAT: A FRUIT HAVING A SINGLE SEED WITH STARCHY  
ENDOSPERM AND HYPOGEAL COTYLEDON

(9) Draw a soaked wheat grain and label the *furrow*, *hairs*, and *embryo* visible through the coat on the convex side. Remove the fused *pericarp* and *testa*. Insert the point of sharp scalpel or needle between the embryo and the endosperm. The embryo will drop off. Note the *scutellum* (cotyledon) which faced the *endosperm*, *radicle* and *young shoot*.

(10) Draw stages of germination showing *adventitious roots*, *coleoptile* and *endosperm*.

## HEREDITY AND EVOLUTION

### *Heredity*<sup>1</sup>

Heredity is the name given to the tendency of like to beget like. To amplify this brief definition into a more satisfactory statement of biological inheritance two qualifications are necessary. It is true that all parent organisms give rise to progeny that resemble them *in a general way*. Members of a well-defined species such as one of the oak trees (e.g. *Quercus pedunculata*) arise only from previous members of the species, and are not known to originate in any other way. It has to be added, however, that *individuals of the younger generation are rarely, if ever, an exact replica of either parent*, and almost always show definite differences even when growing side by side under identical conditions of life. Both these things are familiar to us among our human acquaintances, and are equally true of plants whose reproduction is also sexual. It may not be true of lower plants that have been reproduced by asexual spores; we know little about inheritance in such organisms.

From this standpoint we have also to eliminate the higher plants that have been propagated vegetatively. The plants produced by the "daughter" bulbs of a tulip may resemble their "parent" exactly, but from the point of view of heredity this does not amount to reproduction at all, since no specialised reproductive cells have been involved. The red and white "lady tulip" (*Tulipa clusiana*) has been grown in gardens at least since the seventeenth century and is now cultivated all over the world, but it is a sterile hybrid, and all the plants that have ever been raised must be regarded as separated parts of a single individual, i.e. they constitute a clone (p. 192). All those "varieties" of cultivated plants that are maintained constant by vegetative propagation (notably the potatoes) are similar clones. Not all plants of, say, the "King Edward" clone are exactly

<sup>1</sup> Latin *hereditas*, heirship.

identical in size, number of haulms, colour and so on. Even within the limits of the clone there are fluctuations associated with the conditions of growth; but these, even if the clone is capable of fertilisation, are not inherited.

### *Mendel's Hypothesis*

The simple facts of inheritance mentioned above are among the most obvious that apply to living things and have been realised for a long time. An explanation of them was first arrived at by the Abbé Mendel as recently as 1866, and owing to the obscurity of its publication only became generally known in 1900. The work of the succeeding years has produced a whole science of genetics<sup>1</sup> dealing with variation, heredity and related subjects. The fundamental conceptions of this branch of biology, resting upon the discoveries initiated by Mendel, are dealt with in the following paragraphs.

The new point of view introduced by Mendel that has proved so astonishingly fertile was to consider the plant as an assemblage of unit factors, and to concentrate upon the inheritance of a limited number of factors at any one time, instead of attempting to consider the plant as a whole, as had formerly been done. Further, he built up accurate numerical records of the progeny obtained in his breeding experiments, and for the first time made genetics a quantitative study.

As a result of his experiments he suggested two hypotheses that have since received ample verification and which are called (1) the law of segregation, and (2) the law of independent segregation. In its modern form the *law of segregation* expresses the fact that the hereditary constitution of organisms is composed of a number of distinct and separate units given, for convenience, the name of *genes*. Of the existence of such units there can now be little doubt, but knowledge of their nature, origin and constitution is still next to nothing. Every gene must be supposed capable of reproducing itself, and in the germ cells of a normal diploid plant genes exist in similar *allelomorphic*<sup>2</sup> pairs. Before the formation of gametes the two partner genes separate during cell division so that each gamete has only one gene of each allelomorphic pair. This segregation of individual factors which, after separation may subsequently reassociate, in the same or in *different pairs*, is the segregation referred to in the law's

<sup>1</sup> Latin *genesis*, birth.

<sup>2</sup> Greek *ἀλλήλων* (*allēlōn*), of one another; and *μορφή* (*morphē*), form.



title. There is no fusion or blending of genes at any stage, even while they are associated together in pairs.

The *law of independent segregation* amplifies the first law by stating that the behaviour of the genes in any one allelomorphic pair is independent of the behaviour of those in any other pair. Unlike the first law, this does not have universal application, since *linkage* of genes not in the same pair does sometimes happen during the cycle of reproduction.

### *Mendelian Ratios*

The behaviour of hereditary factors in a few simple and important examples will best illustrate the Mendelian hypothesis.

The plant called "four-o'clock" (*Mirabilis jalapa*) because its flowers open only in the latter part of the day, has two varieties, one with red flowers and one with white. In the plants with red flowers the gene responsible for the formation of the red pigment exists in allelomorphic pairs, the two members of the pair being identical. Similarly in the white variety, the gene producing whiteness in the flowers also exists in identical pairs. It follows that the gametes of the red variety, formed after the separation of the allelomorphs, will all have exactly the same colour genes. Similarly, all the gametes from the white plants can only have whiteness genes. If the two varieties are "crossed", i.e. if a gamete from one is allowed to unite with a gamete from the other, it is found that a gene causing redness is able to form an allelomorphic pair with a gene causing whiteness. The flower colour produced in the resulting diploid plant, with one colour gene necessarily resulting from each plant, is pink; and however many times the cross is made the result is always the same. Such plants are called the  $F_1$  (first filial) generation. Although the parents were homozygous, i.e. with both genes of the allelomorphic pair alike, the  $F_1$  generation is heterozygous, having one redness gene and one whiteness gene in its allelomorphic pair for colour. When the colour genes of the  $F_1$  generation separate prior to gamete formation, they give rise to equal numbers of gametes carrying redness genes and gametes carrying whiteness genes. If the  $F_1$  plants are inter-crossed, there are four possible combinations: one is the union of two gametes bearing redness genes; another is the union of two gametes carrying whiteness genes; the other possibilities are the combination of unlike gametes (white+red and red+white) both of which give pink flowers. The ratios of red : pink : white flowers in a numerous progeny will therefore be 1 : 2 : 1.

These relations are diagrammatically expressed in Fig. 218. It should be specially noted that a proportion of pure reds and pure whites has thus been obtained from the hybrid pinks. The genes for red and white flower colours have not been contaminated by one another in the pink-flowered  $F_1$  generation but have separated out in all their original purity.

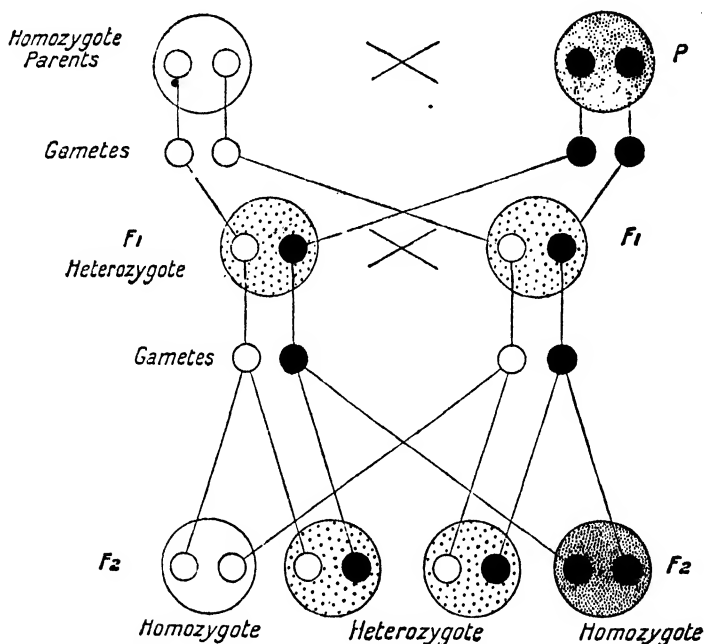


FIG. 218.—Diagram to illustrate the inheritance of colour in the flowers of *Mirabilis jalapa*. The large white circles represent plants with white flowers; the heavily shaded circles with red flowers and the lightly shaded circles plants with pink flowers (heterozygotes). Small circles represent gametes; small white circles represent gametes with gene for white flower colour, black circles represent gametes with gene for red flower colour. After Goodrich, but application adapted.

### Dominance

An example taken from the edible garden pea is especially interesting as being one of those originally worked out by Mendel himself. Mendel worked with two varieties, a tall and a dwarf variety and found that the gene for tallness formed an allelomorphic pair with the gene for shortness. The behaviour of these two genes differs in one remarkable respect from that of the colour genes of

*Mirabilis*. Neither of the colour genes dominated over the other, and the effects of both were apparent in the pink colour of the hybrid flower. In a first cross between a short and a tall pea plant, however, the daughter plants were not of intermediate height, but were all tall and like the tall parent. In describing this state of affairs the gene

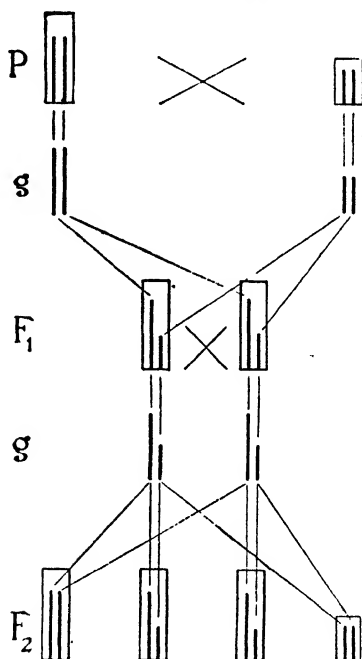


FIG. 219.—Diagram to illustrate the inheritance of height in pea plants. Tall rectangles represent tall plants and short rectangles short plants. Long thick lines represent gametes carrying the gene for tallness and short thick lines represent gametes carrying genes for shortness. P, parent plant.  $F_1$ , first filial generation.  $F_2$ , second filial generation. g, gametes.

for tallness is said to be *dominant* over the gene for shortness, since its effect entirely obliterates the effect of the other in the  $F_1$  generation. Conversely, the gene for shortness is said to be *recessive*. A tall pea plant might therefore be tall for either of two genetical reasons. The allelomorphic pairs controlling its height may consist either of two tallness genes or alternatively of one tallness gene with one recessive shortness gene. A pea plant will only be short when both genes of the allelomorphic pair controlling height are genes for shortness. During crossing the genes assemble and separate just as in *Mirabilis*, but when a mixed allelomorphic pair is present the

character produced will be the same as that produced by a pure pair of dominant genes. In the  $F_2$  generation that results from crossing  $F_1$  plants, the ratio tall : short will consequently be 3 : 1. This will be made clearer by an examination of Fig. 219.

### *Inheritance of Two Pairs of Characters*

Provided that there is no linkage between the pairs, all possible combinations of the pairs will occur on crossing as well as all the possible combinations of genes within their own pairs. Mendel crossed two races of garden peas, a tall one with seeds that were still round when ripe and a short one with seeds that became wrinkled on ripening. He followed the distribution of both the height and seed characters through to the  $F_2$  generation. In the  $F_1$  generation all the plants were round-seeded and tall, those being the dominant characters. The gametes, after separation of their allelomorphic pairs, fell into four genetic classes: tall-round (TR); tall-wrinkled (Tr); short-round (tR) and short-wrinkled (tr). In the symbols in parentheses capital letters indicate dominant genes and small letters the corresponding recessive genes, e.g. t indicates shortness recessive to tallness. On crossing  $F_1$  hybrids, since there was no linkage between height and seed characters, all possible combinations of the four classes could happen. What this amounts to is most easily seen in the table below in which the symbols show the nature of the allelomorphic pairs and the words describe the visible appearances.

		PARENT A			
PARENT B		TR	Tr	tR	tr
	TR	TTRR tall-round	TTRr tall-round	TtRR tall-round	TtRr tall-round
	Tr	TTRr tall-round	TTrr tall-wrinkled	TtRr tall-round	Ttrr tall-wrinkled
	tR	TtRR tall-round	TtRr tall-round	ttRR short-round	ttRr short-round
	tr	TtRr tall-round	Ttrr tall-wrinkled	ttRr short-round	ttrr short-wrinkled

Collecting the results, there are tall-round 9; tall-wrinkled 3; short-round 3; short-wrinkled 1. The fact that Mendel obtained  $F_2$  progeny in these ratios confirms the independent segregation of the

genes concerned. It is also important to notice that in the hybridising of the two original varieties, tall-round and short-wrinkled, two new varieties, tall-wrinkled and short-round, have been created.

### *Linkage*

It must not be supposed that the inheritance of transmissible characters always follows the two simple Mendelian rules. The importance of the rules is not that they are universal but that they provide a first insight into the workings of inheritance and a vantage point from which more complicated examples can be attacked. The next step is to realise that many characters do show a tendency to be inherited together in groups and not to segregate as purely independent units. Thus, in maize plants the genes for deep colour of the grain and fullness of the grain tend to be inherited together, and a fully coloured, shrunken grain is rarely found. A plausible reason for both the independence of some genes and the linkage of others is available and described later (p. 333).

Other complexities revealed by more recent research are the participation of two genes in producing a single visible character, and the dependence of a series of visible characters upon a single gene. Further, the power of forming allelomorphic pairs is not always limited to single pairs of genes. When the two snapdragon species *Antirrhinum majus* and *A. molle* are crossed they produce an  $F_2$  generation showing an enormous number and range of varieties. Some of the plants are even more dissimilar than their parents, and may be hard to recognise as *Antirrhinums* at all. This is due to genes forming new allelomorphic combinations that were not present in either parent.

### *Pure Lines*

By a pure line is meant a race of plants that produces identical progeny when inbred, i.e. when self-fertilised or fertilised by any other member of the line. It represents an ideal of plant breeders, and many of our ornamental garden flowers that are raised annually from seed are pure lines. They have been obtained by inbreeding and selection until a truly homozygous race is the result. Reference to the examples described above will show that only individuals that are homozygous, that is having identical allelomorphs, can be expected to breed true even when self-pollination alone is allowed to take place. It does not, then, matter whether the selected genes are dominant or recessive since they are all alike.

Continual inbreeding in the attempt to maintain a pure line very often results in weakness, loss of fertility or other defects; especially if the characters selected are recessives. There is, for example, a recessive gene in barley which when separated from its dominant suppresses chlorophyll formation. Such a character is lethal and could not exist in a pure line. Many other recessive characters are harmful, though not so completely destructive, and undermine the constitution if they become able to express themselves.

### *Heterosis*

It has long been realised that the crossing of markedly different ("highly heterozygous") parents produces very large and fast-growing offspring. This "hybrid vigour" or heterosis is likely to disappear after a few generations of inbreeding, but can be renewed by further crossing. The explanation of heterosis is unknown, but in practice it is often of much importance in raising commercial seed. An outstanding example is afforded by maize, where first crosses annually produced from selected pure lines are widely used in the following season to obtain high yields of grain for food.

### *Genes and Chromosomes*

The idea of immiscible and segregating hereditary factors put forward by Mendel can be seen from the above examples to give a very plausible basis for the study of inheritance. It is therefore natural to enquire whether any structural units visible, or otherwise detectable, in cells can be identified with these inherited units, the genes. Up to the present, single genes have not been isolated, but there are very good reasons for supposing that chromosomes (p. 49) contain rows of genes lying singly along their length.

Somatic cells are not transmitted to the following generation (p. 112) and their substance cannot carry over the inherited material. This is limited to the germ cells alone. Moreover, the male germ cell, the sperm, often reduced to nothing more than a nucleus, contributes exactly as much genic matter to the zygote as the bulkier egg. In discussing the transmission of genes in the previous sections it was not necessary to distinguish between male and female gametes; each contributed one member of the allelomorphic pair. Of the nuclear structure only the chromosomes appear to persist through all the changes of the nuclear cycle. Their behaviour in passing through the cycle is, moreover, exactly what would be expected of aggregates of genes, and it seems natural to regard

them as the hereditary material broken up into a number of lengths. Their behaviour during the nuclear division is particularly illuminating.

### *Meiosis*<sup>1</sup>

Meiosis is the necessary corollary to the nuclear fusion of gametes. The stage of its occurrence in different plants is shown on page 149. It is most conveniently studied during the pollen production of higher plants though it has also been observed in lower types (Fig. 220). Each pollen mother cell forms a tetrad of pollen grains by a double division. This double division is the meiosis. The prophase of the first division is divisible into the following stages.

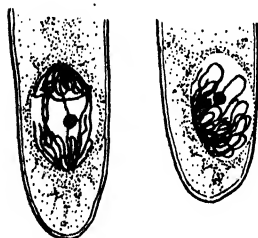


FIG. 220.—Meiosis in antheridium of *Fucus vesiculosus*, prophase on the left and anaphase on the right. After Tischler.

*Leptotene*. At the outset the chromosomes become visible as fine threads which are single, not double as in ordinary mitosis. Each has an uneven granular appearance like a badly strung row of small beads. The granules are called *chromomeres* and at this stage the chromosomes lie more or less evenly distributed through the nucleus. *Zygotene*. The chromosomes come together in homologous pairs, so forming the haploid number of *bivalents*.

*Pachytene*. The paired threads coil round one another, and some chromomeres swell up so that the chromosomes come to have an irregularly thickened shape.

*Diplotene*. The chromosomes fall apart, each chromosome now being visibly double, i.e. having divided longitudinally into two chromatids. As they begin to separate the chromosomes adhere at one or more points and so form crosses or *chiasmata*. The chiasmata are formed because, while the chromosomes were coiled together, two of their chromatids broke between corresponding chromomeres and made a cross joint with new partners (Fig. 221) to which they remain attached when separation begins. If there is more than one chiasma along the bivalent a loop is necessarily formed by the beginnings of separation.

*Diakinesis*. Contraction is completed with the chromosomes still lying more or less evenly distributed.

**METAPHASE**. The centromeres (p. 51) of the paired chromosomes

<sup>1</sup> Greek, making less.

come to lie one on each side of the equatorial plate of the nuclear spindle which is now visible.

**ANAPHASE.** The centromeres travel towards the two poles of the spindle dragging after them their chromosomes which, owing to the crossing over, are now of mixed origin.

As soon as the chromosomes reach the poles a normal mitotic division begins by the end of which a tetrad of cells has been formed with only a single division of chromosomes, the first, meiotic stage being a separation of whole chromosomes, temporarily paired.

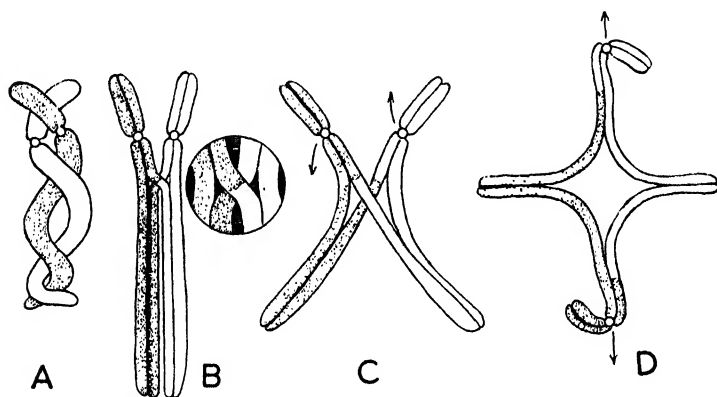


FIG. 221.—Diagram of chiasma formation. A, *pachytene*; chromosomes of a single bivalent coiled round one another. B, *early diplotene*; chromosomes now double and beginning to separate except at the cross join, the chiasma, shown enlarged on the right. C, *late diplotene*; the chromosomes separating and the chiasma sliding towards the far end of the chromosomes. D, *metaphase*. The centromeres, shown as white circles, are now attached to the spindle material and travelling in the direction shown by arrows.

Comparing the cycle of chromosome behaviour revealed in mitosis, sexual fusion and meiosis with the cycle of inheritance brings out the following similarities.

The chromosomes, like the units of inheritance, retain their individuality and do not fuse at any stage. They are associated in homologous pairs during the diploid stages, and are separated during the haploid stages following meiosis, recombining again at fertilisation. The number of genes must, however, greatly exceed the number of chromosomes, which must be supposed to represent chains of genes capable of growing to their original size after division, as the chromatid grows to the chromosome. Genes on different chromosomes will behave independently of one another, like those of the height and seed characters of Mendel's peas; but those that are on



the same chromosome will be linked together. As a result of very extensive experiments, seven groups of linked characters have been recognised in sweet peas, which corresponds with the haploid number of chromosomes. Furthermore, linkage is not complete and absolute, and linked characters, such as colour and fullness in maize are sometimes found to have separated. This can be correlated with the breaking of chromatids and reassembling in new combinations that occur in the crossing over of chiasma formation.

The close correspondence between the behaviour of chromosomes and that to be expected of chain assemblies of genes has done much to increase confidence in Mendel's idea of inheritance by discrete and segregating units.

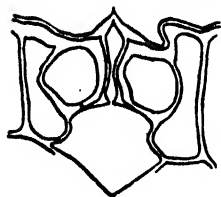


FIG. 222.—Vestigial stoma in the submerged leaf stalk of a floating leaf of *Potamogeton natans*. The stoma is entirely roofed in with cuticle. After Porsch.

#### EVOLUTION

Available evidence is overwhelmingly in favour of the supposition that complex plants such as the angiosperms have evolved by slow degrees from simple ones, perhaps no longer having living representatives; rather than that they have arisen each by a special act of creation. Conviction rests not on any single fact but on an accumulation of corroborative evidence.

Some of the more important points are summarised as follows.

#### *Morphological Evidence*

The range of organic structure that falls within the plant world is immense. As shown in earlier chapters it ranges from simple unicellular forms to complex structures, including many specialised and co-ordinated cells. It is not difficult to imagine that the complex forms have arisen through a progression of simpler ones, more or less resembling the simpler forms now existing. Within a wide group such as the flowering plants many smaller ones exist denoted by some special characteristic such as the succulence of the Cactaceæ and the butterfly-like flower of the Leguminosæ. It is difficult to imagine this family character arising in any other way than from a common ancestor. Frequently such a character can be found with numerous small variations that suggest the resemblances of parents, children, cousins and so forth in a human family. The modifications of flower structure in the Ranunculaceæ (buttercups, kingcups, christmas rose, columbine, *Delphinium*, etc.) is a good example.

*Vestiges.* Many plant organs exist that have every appearance of being vestigial. That is to say they exist, not because they assist the life of the plant, but as the remains of ancestral organs. The stomata found in the submerged leaves of *Potamogeton natans* must have been inherited from an aerial ancestor, and have become sealed up by a continuous sheet of cuticle across the pore (Fig. 222). Many species of the family Scrophulariaceæ (such as the foxglove, *Digitalis purpurea*) have four stamens alternating with the five petals in such a way as to suggest that a fifth stamen is "missing." The related plant *Penstemon* has a vestigial non-functioning stamen (*staminode*) in the expected position. The suggestion is strong that the family descended, i.e. has been evolved, from a five-stamened ancestor.

Most striking of all, perhaps, the whole long story of sexual reproduction in plants can only be understood as a continued modification of ancestral structures no longer adequate for survival.

*Embryology.* Some plants pass through a series of developmental changes of form before they arrive at their mature structure. Many cypresses have youth forms in which the leaves are simple and free. The closely appressed leaves fused with the stem are found only at a later stage. One of the most striking examples of such a change occurs in the genus *Acacia*. The young seedlings have the pinnate leaves so typical of many members of its family, the Leguminosæ (Fig. 223). The adult plant has *phyllodes* only, i.e. petioles that are flattened into the semblance of a simple, lanceolate lamina. The seedling leaves drop away; but they seem to hint at the descent of *Acacia* from a leguminous ancestor with pinnate leaves.

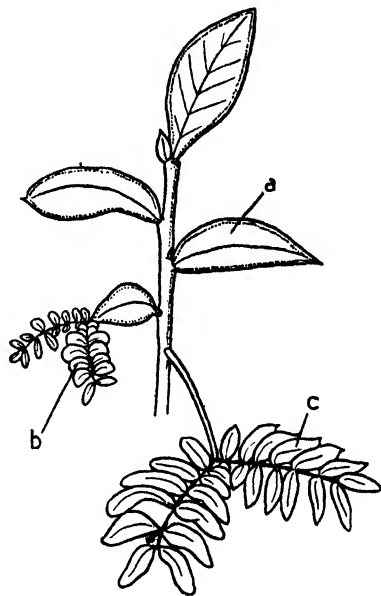


FIG. 223.—Young plant of *Acacia pycnantha*. a, phyllode; b, leaf with pinnate lamina and flattened petiole; c, pinnate leaf. Nat. size.

*Historical Evidence*

Plant evolution is too slow for it to be easily observed around us; but the fossil record is instructive. Unfortunately, the loose straggling form of plants leads to fossilisation in small disjointed fragments and it is rarely that a complete plant can be reconstructed. Fragments of plants belonging to existing angiosperm stocks can be found from the Cretaceous era; while in the Jurassic strata plants resembling angiosperms are found, but none in the earlier rocks. It is, relatively speaking, a young class. In the coal measures abundant remains are found of plants of the Pteridophyte class, which also extend back into the Devonian. Through this long period it is possible to trace the rise and fall of some of the Pteridophyte races; notably the Equisetales, represented in the coal measures by numerous large trees, and now surviving only in the degenerate "horse-tails." Such phyletic histories exist far more abundantly among animals like shell-fish, whose form and habitat are so much more favourable to fossilisation.

*Geographical Evidence*

Groups of closely similar plants often have a restricted and more or less continuous distribution, even although it occupies only a very small proportion of the suitable habitats available. This suggests that the group has arisen in some one spot from a single ancestor, and has subsequently slowly spread and undergone further modifications. Thus Darwin found that most of the plants of the Galapagos Islands, 500–600 miles west of Chile, were not themselves found outside the islands, although evidently related to those of the American continent.

*Selection and Breeding*

Although it is so difficult to watch evolution happening naturally, it can certainly be brought about artificially. Special strains of plants and animals are bred by cross-fertilisation and selection of progeny for further breeding, until the final production is often unrecognisable as a descendant of the original wild plant or animal. There are dozens of artificially evolved wheats now in cultivation. The wheat found in Egyptian tombs and granaries is different from all of them and nobody now knows what the original wild wheat plant looked like. This artificial evolution ("breeding") is the basis of numerous industries. Special dogs are bred for sheep-driving, racing and nursing in the lap; special flowers to make the brightest show in

gardens; special vegetables and fruits to provide food at different seasons, and special yeasts to make different sorts of beers—to mention only a few examples. The fact that evolution can be brought about artificially is not by itself a proof that it happens naturally; but living things lend themselves so readily to the process, having within themselves the potentiality of varying, that it is evident they are likely to undergo spontaneous evolutionary changes.

Charles Darwin gathered together all the above points and many more. He gave a great wealth of detail concerning each, which he had patiently gathered over half a lifetime. He did not invent the idea of evolution, which in fact seems almost as old as human thought, but he converted it into a well-founded scientific hypothesis.

#### THE METHOD OF EVOLUTION

It is one thing to show that evolution has taken and probably still is taking place. It is quite another to explain the method or methods by which it has been brought about. The study of the mechanism of evolution really involves two different problems; firstly how new forms of organisms, able to propagate their kind, *originate* and secondly which of them will be able to survive, *establish* themselves, and so give rise to new races.

An answer to either one of these problems, however satisfactory, is not an answer to the other and therefore only half an explanation of the method of evolution.

#### *The Origin of New Varieties*

New varieties are possible because existing ones show to a greater or lesser degree the property of producing variations that can be transmitted to their progeny; variations, that is to say, of their gene assembly (genotype). Fluctuations of the soma in response to environmental conditions are non-transmissible and therefore of no evolutionary significance.

*Mutation.* Occasionally a new character or even combination of characters appears suddenly among the more or less standard members of a pure race. This is familiar to gardeners and plant breeders who call the new forms *sports*; all the climbing roses are tall-growing sports of the corresponding bush kinds. Sometimes the new character is inheritable, like the changed colours that occasionally appear in self-pollinated sweet peas. The products of suddenly appearing and inheritable changes of this kind are called *mutants*. Since mutation can appear in a pure line it must involve a change in

one or more genes. How this comes about is unknown, though some changes of this kind can be induced artificially by means of X-rays. De Vries first studied mutation in the progeny of a plant of evening primrose, *Oenothera lamarckiana*, and pointed out its significance in the study of evolution.

It is necessary to distinguish clearly between genes, which are the hereditary material of the plant, and the characters that appear superficially. An observable character *may* be the result of the activity of only a single kind of gene, e.g. the red or white flower colour of *Mirabilis jalapa*; but this is exceptional rather than the rule. Usually an observable character is affected and controlled by several genes. Complete dominance or the entire suppression of external effect, is not the only way in which one gene may modify the effect of another, and frequently the results are more balanced. The influence of the external environment must also be considered. The recessive barley gene that controls chlorophyll formation only leads to a completely albino plant below 6.5° C. and above 18° C. normal chlorophyll formation takes place. The alteration of a single gene, even though the total number possessed by a plant is probably not very great, will, therefore, not be likely to lead to any very striking change of visible characters. This is important because everything indicates that evolution goes on by small steps. When larger changes do occur they are almost always unfavourable, and lead to the dying out of the race.

*Hybridisation.* New varieties may also arise in less drastic fashion by hybridisation (cf. p. 330), especially where there are numerous allelomorphic pairs of genes producing interacting external results; or where many genes are capable of forming allelomorphic pairs indiscriminately, as in the *Antirrhinums* described on page 330. A great wealth of new forms is thus produced differing from both parents to a marked degree.

### *Natural Selection*

Competition for existence is very severe among plants (cf. p. 321). New organisms will therefore tend to survive and to displace old ones if they are on the whole better adapted to their surroundings. Individuals that have a gene complex giving them any special advantage will generally form a larger proportion of the ancestry of the next generation than those without it. If their special character is inheritable the new race will gradually emerge from the old and an evolutionary change will then have been completed. The inevitable

operation of this *natural selection* in a crowded world was very fully appreciated by Darwin, who first brought it to the notice of biologists. He thereby provided a satisfactory key to the principle underlying the *establishment* of new species.

### *Survival of Sexual Reproduction*

It has often been thought remarkable that sexual reproduction should be so frequent among living organisms in spite of its obvious hazards, especially when it has to be adapted to a subaerial environment. The possibilities of recombination of genes, which only sexual reproduction affords, is clearly the basis of an enormously greater number of varieties than is possible with reproduction of the asexual sort. There must always, therefore, be a much wider variety of sexual than of asexual material for selection to work upon and, for this reason, it is not surprising that the majority of existing organisms show sexual methods of reproduction.

### *Fitness and Adaptation*

Many organisms and parts of organisms are very admirably fitted for the roles they play. To take a single example, the parachute of dandelion fruits is a very efficient arrangement for wind carriage. Such excellent adaptation is far from being a general rule; and as an example on the other side may be mentioned the metabolism of yeast and of many bacteria that leads them to form toxins to which they themselves fall victims. Generally speaking, the more highly evolved an organism becomes, the greater is the fitness of itself and its parts to secure their method of existence. If attention were strictly limited to the higher types, it might be possible to imagine that each was designed to fulfil a preconceived purpose and that an answer could be given to the question "What is it for?" A study of a range of simpler and more primitive organisms, such as was undertaken in the earlier chapters, should remove this idea. Instead, it will be realised that the fitness of closely adapted organisms comes from a weeding-out of the failures among a vast array, each individual organism being the result of a random assembly of genes. Fitness is, genetically speaking, the chance result of a fortunate combination.

## Chapter XXVI

### YEAST

Many of the living cells of the higher plants do not contain chlorophyll in meristems, roots and other underground parts. All such cells have to be fed with sugar from the green cells, and with nitrogenous and other substances from the soil.

There are some plants that have no green cells: a few degenerate seed plants; the great group of the *Fungi*; and the unicellular plants known as *Bacteria*. All these colourless plants, with the exception of a few bacteria, obtain the materials for the formation of new protoplasm and the carrying out of their life processes by absorbing soluble organic substances from outside. This they do either as *saprophytes*<sup>1</sup> drawing on non-living sources, or as *parasites*<sup>2</sup> gaining nutriment direct from the body of a living host.

The yeasts (*Saccharomycetes*)<sup>3</sup> are unicellular fungi with which it is convenient to begin the study of colourless plants. There are many different kinds of wild and cultivated yeasts, some of them differing conspicuously in appearance, cell size and activities. Most are saprophytic, but a few are parasites and the causes of some animal diseases.

#### *Structure*

The individual yeast cell is spherical or ovoid (Fig. 224) and about 8–12  $\mu$  in diameter. This is small compared with the cells of higher plants (around 100  $\mu$ ), but about the same size as *Protococcus*. The yeasts all have a thin wall and a relatively wide lining of cytoplasm surrounding a central vacuole. At one side of the vacuole is the nucleus with dark staining chromatin strands that also extend round the vacuole (Fig. 224, chr.). Other small granules and droplets

<sup>1</sup> Greek σαπρός (sapro), rotten; and φυτόν (phuton), plant.

<sup>2</sup> Greek παρά (para), irregular; and σίτος (sitos), food.

<sup>3</sup> "Sugar fungi."

appear in the cytoplasm, varying with the metabolic condition of the cell. These are mainly glycogen—a polysaccharide resembling the dextrins and fats.

### Habitats

Wild yeasts are found in sugary exudations of plants, such as the nectar of flowers and on the surface of grapes and other fruits with broken skins. Their spores are almost universally present in the air and any exposed sugary solutions, jams, syrups or culture plates very soon acquire a yeast flora. The yeasts, like many of the higher plants, cereals and fruit trees, for example, are better known in the domesticated than in the wild state, and are cultivated for many different uses (p. 344).

### Nutrition

Yeasts can be found upon a variety of organic materials, and do particularly well where free sugar is present. They can be cultivated upon a solution containing the usual inorganic salts with the addition of ammonium tartrate, an organic substance simpler than

sugars though with some similarities to them. The tartrate ion yields the necessary carbon and the ammonium the necessary nitrogen. Yeast only grows very slowly in such a medium, and if sugar is added it grows and multiplies much faster.

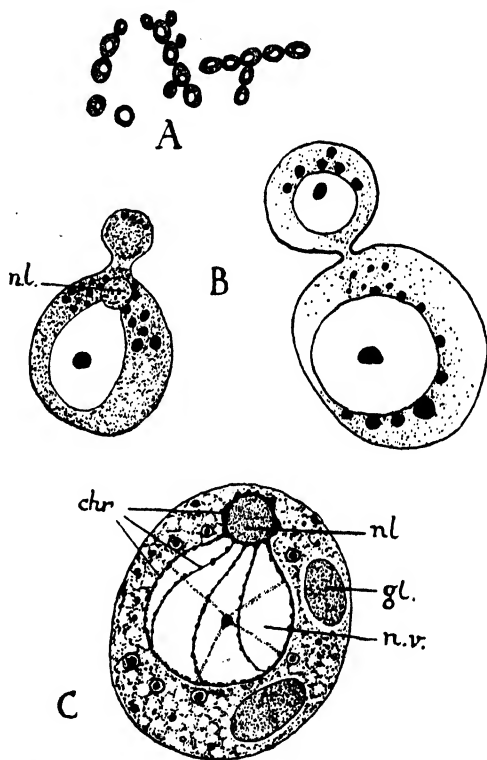
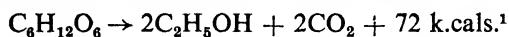


FIG. 224.—*Saccharomyces*, yeast. A, cells budding and forming chains. B, two cells forming buds; *nl*, nucleus. C, a single cell very much enlarged; *nl*, nucleus, *chr*, chromatin strands; *gl*, glycogen granules; *nv*, vacuole. After Wager and Penistone.



*Metabolism*

Yeast is characterised by an outstanding capacity for breaking down sugar in the absence of oxygen. This is a property possessed by the great majority of plants in varying degrees; but when yeast cells are inoculated into a sugar solution its decomposition is rapid and thorough. The principal products are carbon dioxide and ethyl alcohol and the process is called alcoholic fermentation. It proceeds almost quantitatively according to the equation



About 2 per cent. of the sugar is unaccounted for, and that is the maximum amount that might be utilised by the yeast for growth. It has, in fact, been observed that under anaerobic conditions, however vigorous the fermentation may be, the yeast does not multiply appreciably. Large amounts of energy are degraded, but it is not at present possible to show that fermentation serves any purpose essential to the existence of the yeast plant. It is possible that yeast is no better adapted to a sugar solution than a bull to a china shop.

Most plants under aerobic conditions cease to form alcohol or other products of fermentation; but yeast goes on. At the same time it respire, i.e. it carries out a process similar to respiration in the higher plants, converting some of its sugar to carbon dioxide and water. There is simultaneously a transformation of energy that can be applied to growth and synthesis. One result of this is that the cells begin to accumulate glycogen, which they synthesise from alcohol. They also grow and divide, so that the colony increases and fermentation goes on more furiously than ever. In the practice of brewing, aeration has to be controlled in such a way that enough oxygen is given to promote rapid growth, but not enough to reduce alcohol production. Alcoholic fermentation of sugars by yeast bears some resemblance in its mechanism to the aerobic and anaerobic respiration of the higher plants. The most striking resemblances lie in the catalytic part played by the phosphate ion and the synthesis of hexosediphosphate, which appears to be the substance actually split in all three processes. Zymase is a collective name for the series of enzymes that catalyses alcoholic fermentation: many of its constituents such as zymohexase and carboxylase are present both in yeast and in the higher plants. The nature of yeast respiration is more uncertain.

<sup>1</sup> Free energy under biological conditions, not heat of reaction.

### Life Cycle

The cells of *Saccharomyces* multiply by budding (Fig. 224 A and B). A tiny area of the cell wall, usually at one end of the cell, softens and is pushed out into a bud by the cell turgor. The bud increases until it is the size of the parent cell and, in baker's yeast, is finally nipped off. When the growth of brewer's yeast is very rapid in a sugar solution the cells remain attached to one another in chains, which branch where a cell has thrown out more than one bud (Fig. 224 A). The nucleus divides, probably with an accurate division of the genetic material, and one daughter nucleus migrates into the bud as it forms.

**Spore Formation.** Under favourable conditions the multiplication of yeast cells goes on very rapidly, but when conditions deteriorate a change sets in and the cells are seen to be forming spores. Under natural conditions this occurs towards autumn, and it may be induced in culture by partial drying out on the surface of a cut potato or similar medium. The cells perform a double division: the protoplasm withdraws from the wall, rounds off around the four daughter nuclei (Fig. 225), and secretes a thick wall round each spore. The four of them remain enclosed in the original wall, and in this state pass through the winter or other unfavourable season. In spring the spores germinate and bud off new cells.

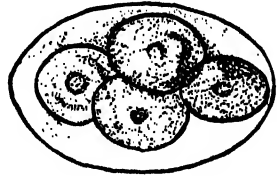


FIG. 225.—*Saccharomyces* spores. Four walled spores contained within the parent envelope. Highly magnified.

**Sexual Fusion.** Sexual fusion occurs between pairs of yeast cells which are potential gametes. The fusion may take place between adjacent spores as they germinate (Fig. 226, top line), so giving rise to a diploid population. Fusion may, however, be delayed and take place at any time in the active season right up to the time of spore formation (Fig. 226, lower lines). Spores that germinate without immediate fusion give rise to haploid cells. Most natural yeast populations are therefore mixtures of haploid and diploid individuals, the diploid cells being relatively large and ovoid and the haploid cells small and more spherical. Whatever the exact occasion, fusion occurs at some time prior to spore formation, and the cells become diploid. The double division leading to spore formation is probably a meiosis and the spores are always haploid. A number of strains are always present in natural populations and can be distinguished in

the haploid state. They may be divided into two classes. Vigorous growth and spore formation often result only when strains from different classes unite. Union of strains within either class produces only feeble cells incapable of spore formation. This is reminiscent of the hybrid vigour found in the higher plants (p. 331).

### Utilisation of Yeasts

The ancient art of *brewing* has become a branch of applied botanical science. The starch and proteins of barley grains are hydrolysed to a mixture of sugars and soluble nitrogenous substances by a controlled germination on the malting floor. The enzymes are then inactivated by drying the malt in kilns. The dried

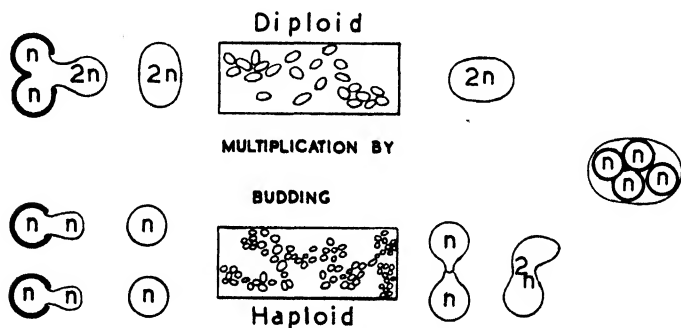


FIG. 226.—Life cycle of *Saccharomyces*, showing different occasions of sexual fusion.  $n$  = haploid;  $2n$  = diploid cells.

malt is steeped with warm water, boiled with hops to extract their bitters, sieved and run off into vats, where the extract is cooled and a pure culture of yeast added. The sugars are fermented, heat and carbon dioxide come off in large quantities and are removed by currents of cold air. The intrusion of bacteria and wild yeasts is rigorously guarded against until fermentation has reached the desired point. Spirits are obtained by distilling out the alcohol from the watery mixture.

*Wine making* from the fermented juice of grapes depends upon the wild yeasts present on the skins, and as soon as the grapes are crushed fermentation begins. Wine making is still more of an art than an applied science, and the infinite variety of wines depends upon vagaries of traditional practices, soils, climates and vines. The utilisation of yeast in *bread making* rests on its production of carbon dioxide by the fermentation of small quantities of the bread sugars. The resulting gassing forms bubbles in the hardening dough,

and so makes the bread light and palatable. Since it goes on aerobically there is little alcohol formation and baker's yeast is a selected variety to this end.

Yeast is a very convenient source for the extraction of enzymes and vitamins that cannot be artificially synthesised. It has therefore a great and increasing variety of applications in dietetics, medicine and near-medicine. It was Buchner's attempt in 1897 to preserve a yeast extract for medicinal purposes that led to the discovery of zymase, one of the first enzymes to be isolated from the living cell. A hitherto wild yeast, a species of *Torula*, has been found to form its proteins abundantly from simple ammonium salts mixed with molasses (uncrystallisable sugar residues) and distilling wastes. It is being applied to the production of proteinaceous food for animals and man from these inexpensive by-products.

### Practical Work

(1) Place a drop of brewer's yeast on a slide, cover and examine with the high power. Look for *branched chains* due to budding. Draw an individual cell marking *wall*, *cytoplasm* and *vacuole*. Look for the *nucleus* beside the vacuole. Apply Schulze's solution, and note that the wall turns blue (cellulose).

(2) Mount a little yeast as before and irrigate with very dilute iodine. Look for *glycogen granules*, which turn brick red, in the cytoplasm.

(3) Crumble about 5 gm. baker's yeast into 25 ml. of a 10 per cent. glucose solution, and put the mixture into a large test tube. Fit a cork with a delivery tube bent at a right angle and let the end of this open into a second tube containing baryta or lime-water. Put the tube containing the yeast into a water bath at about 35° C. Bubbles of carbon dioxide will form in the sugar solution and after a time the lime-water will become milky. After 1 or 2 hours uncork the tube; the smell of alcohol will be noticeable.

## Chapter XXVII

# BACTERIA AND VIRUSES

### *Size and Structure of Bacteria*

Bacteria are extremely small, the diameter of an average bacterial cell being only about  $1\ \mu$ , far less than that of other unicells, and almost at the limit of normal microscopic vision. The visible bacteria may be roughly classed according to their shapes as *cocci*,<sup>1</sup> which are spherical; *bacilli*,<sup>2</sup> straight cylindrical rods; and *spirilla*,<sup>3</sup> curved rods or corkscrews. The method of aggregation may also be indicated by the prefixes *strepto*-<sup>4</sup> indicating in curved chains, and *staphylo*-,<sup>5</sup> in clumps. Fig. 227 A shows *streptococci* and *staphylococci* from pus.

Each bacterial cell consists of a minute mass of protoplasm. Some at least of the contents stain heavily with nuclear stains; but the distribution of the chromatin in so small a cell is difficult to determine. The nature of the surface is also rather uncertain; it is not composed of cellulose, and may be more like the surface of an animal than of a plant cell. In some kinds of bacteria a much thicker wall, the capsule, is present. It is mucilaginous, contains polysaccharides, and causes the whole colony of cells to adhere together in a *zooglæa* visible to the naked eye and slimy to the touch. Extremely delicate threads of protoplasm project either singly (as *flagella*), or in groups (as *cilia*), from the surface of some species (Fig. 227 B, C, F). They can be detected only by special methods of staining.

### *Movement and Response to Stimuli*

Many kinds of bacteria move actively in liquid media such as body fluids and the soil solution. This may be effected by means of

<sup>1</sup> Greek *κόκκος* (*kokkos*), a berry.

<sup>2</sup> Latin *bacillum*, a little staff.

<sup>3</sup> Little spirals.

<sup>4</sup> Greek *στρεπτός* (*streptos*), bent.

<sup>5</sup> Greek *σταφύλη* (*staphulê*), bunch of grapes.

the cilia and flagella; but spirilla appear to move by waves of contraction and expansion of the cell as a whole. Motile bacteria move as a rule either up or down concentration gradients of substances—positive and negative chemotaxis. *Bacterium termo* is especially sensitive to free oxygen and clusters round any point at which oxygen is being liberated.

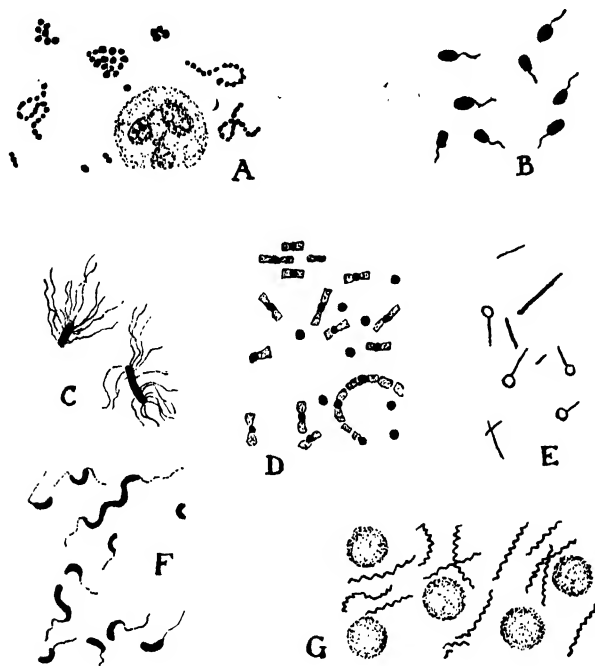


FIG. 227.—Bacteria. A, *Staphylococci* (groups) and *Streptococci* (curved chains) from pus. The large spherical body is a pus corpuscle. B, *Nitrosomonas*, a nitrifying bacterium from soil, with a single flagellum. C, *Bacillus typhosus* (typhoid germ) with flagella. D, *Bacillus anthracis* (anthrax germ) showing spores in the centre of each cell. E, *Bacillus tetanus* (tetanus germ) with spherical spores. F, spirillum of cholera. G, *Spirochaete pallida*, the germ of syphilis. After Muir and Ritchie. All  $\times 1000$ .

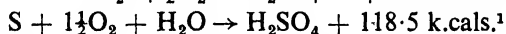
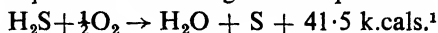
### Nutrition

*Photosynthetic bacteria.* All bacteria are devoid of chlorophyll. It has recently been discovered that a few possess similar pigments, bacteriochlorophylls, by means of which they photosynthesise. The *Thiorhodaceæ*, green and purple sulphur bacteria, reduce carbon dioxide in the light by means of sulphuretted hydrogen ( $H_2S$ ) liberating sulphur instead of oxygen. They occur in fresh and salt

water muds, and represent a small and far from typical group of bacteria.

*Chemosynthetic bacteria* are also autotrophic, building up their organic materials from carbon dioxide. They do this, however, with the assistance of energy other than sunlight, viz. with the energy of exergonic chemical reactions, which they are able to couple with carbon dioxide reduction. In this they are probably unique. A well-known example of this class is *Beggiatoa*, a sulphur bacterium that inhabits stagnant ponds. It oxidises sulphuretted hydrogen to free sulphur which is deposited as granules in the cells. At the same time carbon dioxide is reduced and organic materials formed. In the absence of further sulphuretted hydrogen the sulphur granules disappear from the cells, being further oxidised to sulphuric acid which escapes to form salts in the surrounding water.

The two reactions proceed according to the equations:



There are numerous other chemosynthetic bacteria oxidising thiosulphate, tetrathionate, ammonium thiocyanate, ferrous iron, free hydrogen, carbon monoxide, methane, formaldehyde and other substances. Some that are more important in their effects upon the outside world are described on page 354.

*Saprophytic bacteria* are more numerous. They must absorb ready-made organic foodstuffs that pass their surface membranes in solution. They are common inhabitants of rich soils, hay, dunghills and any other putrescent material. They break down the body substances of dead plants and animals, and so obtain the sugars and soluble nitrogenous materials necessary for the construction of their cells. The bacteria responsible for putrefaction are of great importance in the circulation of nitrogen (p. 353).

*Parasitic bacteria* are also very numerous and obtain their organic foodstuffs direct from living hosts. They are mostly parasitic on animals, being adapted to living at a temperature around blood heat (about 37° C.) and at a strictly neutral pH, more common in animal than in plant cells which tend to be somewhat acid. Being unicellular, bacteria are also readily distributed in the blood stream once they get into it. Many of the parasitic bacteria are the agents of serious human and animal diseases (p. 357).

*Bacillus tetanus* is a common inhabitant of manure heaps and of rich garden soils where it lives saprophytically. If it enters the

<sup>1</sup> Decrease of free energy, not heat of reaction.

human body through any small break in the skin it becomes a parasite, causing the dangerous disease of lock-jaw. A dab of iodine before it has become disseminated in the blood stream will coagulate its proteins and prevent its undesirable activity. Like many other bacteria it passes very readily from saprophyte to parasite according to the situation in which it finds itself and, from the standpoint of general biology, the difference is indeed rather slight.

The form in which food is absorbed by any bacterium, to whichever of the above classes it belongs, must be either gaseous or liquid, and for this reason bacteria are classified as plants.

### *Respiration and Synthesis*

The heterotrophic bacteria break down and absorb a great variety of organic substances. In so doing they obtain materials for their respiration and the building of their own body substances. Many are able to break down sugars and oxidise the products in ways resembling the alcoholic fermentation of yeast and the respiration of the higher plants. In so doing they produce an enormous variety of products; different strains of bacteria have characteristic products under given conditions. On cultures containing glucose *Bacterium acidi propionici* produces propionic, acetic and succinic acids as well as carbon dioxide. Butyric acid, acetone and free hydrogen are a few other products of bacterial metabolism. If oxygen is present these substances are oxidised more or less completely, apparently by enzymes resembling those of the higher organisms, so affording the necessary energy for the cell syntheses. The link between oxidation of plastic substances and synthesis of cell materials is thus of the same general nature as in higher organisms, but bacteria show a far greater variety of reactions than the more or less standardised ones of the higher plants and animals. Putting it in another way, their metabolism is less rigidly selected, and they still provide humble examples of methods of life that cannot succeed on a wide scale. An example is afforded by the obligate anaerobes, like the *Clostridia*, whose growth is actually stopped by exposure to oxygen and can only go on in places where free oxygen is almost entirely excluded. Their respiration must obviously differ from that of aerobic organisms, and depends on combined oxygen in nitrates and similar substances.

The autotrophic bacteria, both photo- and chemosynthetic, probably behave in rather similar ways, but it has not yet been shown conclusively that they form sugars from the carbon dioxide



that they fix, although it seems probable. Even in the higher plants it is possible that substances other than sugars contribute a quota towards the respirable materials, and in bacteria it is well-nigh certain.

### *Fermentation*

The anaerobic breakdown of organic materials by bacteria leads to large-scale changes in the external medium, just like the total breakdown of sugar to alcohol by yeast. Bacteria in milk ferment its sugar to lactic acid which makes it sour: others in butter ferment its fats to butyric and other acids that make it rancid. The turning bitter of cut fruits, like melons, and the putrefaction of meat are also due to bacterial fermentations.

Some fermentations are turned to practical account. Cheese-making, tobacco-curing, flax retting (isolating the fibres from the soft parts), composting are a few of the processes that utilise them. Vinegar is made by allowing *Baeterium aceticum* to act on alcohol, converting it to acetic acid  $C_2H_5OH + O_2 \rightarrow CH_3COOH + H_2O$ . This is not, strictly speaking, a fermentation, but an incomplete oxidation.

### *Reproduction*

The bacteria multiply by simple division of the cell into two and separation of the daughter cells so formed. Sometimes the cell grows to a larger size than the normal before division; but simple binary fission without complications seems to be the general rule among bacteria. The daughter cells of a bacillus frequently remain together for a time after division, so that lines of cells having the form of jointed rods are produced.

In most bacteria growth and multiplication proceed with great rapidity. Under very favourable conditions a bacterium may reach maturity and divide in twenty to thirty minutes. If division takes place only once an hour, seventeen million individuals will have arisen from a single cell in twenty-four hours. The chief factors which control the rate of multiplication are temperature, food supply and the presence or absence of poisonous *toxins* produced by the bacteria themselves.

### *Spore Formation*

In certain species of the simpler bacteria, chiefly bacilli, spores are produced under adverse conditions. These spores are formed in the

same sort of way as yeast spores, by the aggregation of the protoplasm at a given spot in the cell, the protoplasm of the spore being surrounded by a dense wall. Only one spore (Fig. 227) is formed in each cell, either in the centre or close to one end. When the spore comes into conditions suitable for growth, the spore wall is split and a new vegetative cell protrudes, assuming the form characteristic of the species.

Bacterial spores are by far the most resistant form of living protoplasm known. Many can withstand for some time exposure to dry heat of considerably over  $100^{\circ}\text{C.}$ , while most vegetative forms are quickly killed at  $50^{\circ}\text{C.}$  Some spores can even withstand immersion in boiling water for several minutes; they may remain alive in a dry and inactive condition for years. The great difference between the powers of resistance of vegetative cells and spores is illustrated by the anthrax bacillus (*B. anthracis*). The active vegetative cell is killed by two minutes exposure to 1 per cent. carbolic acid, while spores resist immersion in the same solution for as much as fifteen days. Vegetative forms can, however, withstand extreme cold for a long time, for instance the temperature of liquid air ( $-190^{\circ}\text{C.}$ ), for twelve months.

### *Dispersal*

Spore formation is not a means of *multiplication* in bacteria. Only one spore is normally formed by the bacterial cell and the growth and division of the organism is completely arrested until the spore germinates. The spore condition is the *resting stage* of the bacterium, enabling it to stand conditions unfavourable for vegetative growth and multiplication. Spores are, of course, an important means of *dispersal* for the forms which produce them, since they are passively carried about in currents of air without injury, whereas vegetative bacterial cells will sooner or later be killed by drying up. But only comparatively few species of bacteria are known to produce spores, most kinds being dispersed entirely by means of the ordinary cells. Bacteria often get into the air by detachment of minute particles from the surface on which they are growing. Such particles form part of the dust of the air and practically all air at low levels, except over mid-ocean, contains more or less dust. Dust is carried about in currents of air and is often blown by the wind for very long distances. When the air becomes comparatively quiet, the particles drift slowly down and settle. Any living cells which they carry, vegetative bacterial cells, bacterial spores or fungal spores, will grow

if they find themselves in suitable conditions of moisture, food supply and temperature. In such conditions spores will germinate and such vegetative cells as have not been killed by drying up will grow and divide.

### *Sterilisation*

Owing to the copious distribution of their cells and spores, bacteria cannot be eliminated over any wide area. Their destruction or removal from any enclosed space may be a matter of great importance and may be achieved in a number of ways.

*Heat sterilisation* is achieved by the use of temperatures at which even bacterial spores are unable to survive. It can usually be effected by dry heating at  $160^{\circ}\text{C}$ . for half an hour or at  $180^{\circ}\text{C}$ . for ten minutes. It is often more convenient to use superheated steam under pressure in an autoclave, and then five or ten minutes at about  $120^{\circ}\text{C}$ . suffices. If a liquid is to be sterilised it may be boiled at  $100^{\circ}\text{C}$ . It is then necessary to repeat the process three or four times to kill any bacteria that may have survived the first boiling as spores.

*Antiseptics*. Bacteria are readily killed by a whole range of coagulants such as iodine, carbolic acid (phenol) and mercuric chloride, by oxidisers such as hydrogen peroxide and permanganate and by many other poisons. The use of such antiseptics is often the most convenient method of sterilisation where the presence of the added substance is not objectionable.

*Filtration*. A rough sterilisation of a liquid may be obtained by forcing it through unglazed porcelain of very fine texture. The method is sometimes used to sterilise tap-water by attaching a porcelain "candle" to the tap. It is uncertain because of the inequalities in the size of the pores in even the finest porcelain. Bacterial filters of thick cellulose pads are nowadays used in specially constructed funnels and give good results. All the receiving apparatus must first be sterilised by heat.

*Sunlight* is lethal to some bacteria and can be used to eliminate them; *oxygen* destroys anaerobic bacteria such as the tetanus bacillus. *Bacteriostatic substances* produced by moulds and other plants are mentioned on p. 372.

### *Pure Cultures*

Bacteria exist naturally in mixed associations of many kinds. The discovery of methods of complete sterilisation make it possible to grow isolated strains in pure culture, without which satisfactory study of bacterial activities has proved impossible. The making of

pure cultures is based on the fact that if a suspension of bacteria in a liquid is diluted with a large excess of sterile water and the bacteria evenly distributed through it by shaking, each drop of the mixture will contain only a few cells or even only a single organism. Such a drop added to a sterilised culture medium will probably give rise to a growth consisting of one sort of bacterium only. The culture medium is usually solidified by being mixed with an agar jelly, on which the individuals then multiply and form colonies that become visible as dots. Further transfers and sub-cultures can be made, and the growth and properties of the pure strain of bacteria studied.

### *Species and Strains*

So far as we know, bacterial species are about as constant as those of other organisms, but visible structural differences are not adequate to distinguish them. Other characters, such as differences in staining and in the type of growth made on different cultural media, have to be used for accurate bacterial diagnosis.

Although the well-known bacterial species appear to be clearly distinguishable from one another and do not interchange, they have very considerable powers of adapting and adjusting themselves to changed circumstances. These adjustments do not include sudden radical changes of nature or structure, but the bacteria are markedly more adaptable and less adapted than the higher plants. This is particularly noticeable in their reactions to their environment. The nutritional requirements of the higher plants are rather fixed and rigid; but bacteria are capable of adjusting themselves to considerable changes of their culture media. For example, cultures of *Bacterium coli mutabile*, growing on glucose and asparagine, can be "trained" to utilise ammonium sulphate as nitrogen source in place of their accustomed asparagine. A similar fact of great importance in medicine is that bacteria can become tolerant of substances which at first were poisonous to them. Strains resistant to penicillin (p. 373) are already beginning to appear. The nature of the strains thus produced is sometimes uncertain; they may be genetically pure lines such as are formed by selection among the higher plants, or they may be members of the general bacterial population automatically adjusting to a particular set of circumstances.

## THE CIRCULATION OF NITROGEN

### *Putrefaction*

The nitrogen locked up by plants and animals in their proteins is returned to circulation after their death by fermentations carried on

by a large collection of putrefactive bacteria. Many products are formed including the characteristic evil-smelling gases and, most important of all, large quantities of ammonia forming ammonium compounds in the soil. In the metabolism of the putrefactive bacteria themselves, the proteins supply energy and body materials. Many of these bacteria afford good examples of bacterial adaptability. It has been noticed that, if proteinaceous materials are scarce and carbohydrates abundant, they cease to produce ammonia, but absorb nitrogen compounds like other plants and obtain energy from sugars.

The activity of putrefactive bacteria is stopped—like that of other bacteria—by antiseptics or by heat, and it is slowed down by cold. The use of refrigerators for keeping meat and other foodstuffs depends on this fact. Heat sterilisation is used in bottling and canning. A natural preservation results from the formation of antiseptic substances in peat bogs, and the bodies of engulfed animals are often preserved for many years. The body and accoutrements of a Roman soldier recovered not long ago from a Yorkshire bog were in a good state of preservation.

### *Nitrification*

The action of putrefactive bacteria in a fertile soil continuously converts the humus—the decaying organic debris—into simple ammonia compounds, especially ammonium carbonate. This is an oxidisable substance, and is utilised by *Nitrosomonas* (Fig. 227 B) in chemosynthesis. The action is specific to ammonium carbonate which is oxidised to nitrite. This in turn serves as a material for chemosynthesis to *Nitrobacter*, and is further oxidised to nitrate. The results of these activities are the growth of the bacteria by means of the chemosynthesis and the formation of nitrates in the soil containing them. Carbon dioxide is necessary for the bacterial growth, but light is unnecessary and even harmful. Some sorts of protein, such as gelatine, are also poisonous and, more important in soils, any form of acidity. In sour soils nitrification is greatly reduced. In good soils it is rapid, and the soluble nitrogen compounds accumulate mainly as nitrates. Green plants absorb both ammonium salts and nitrates and build them up anew into proteins.

### *Nitrogen Fixation*

The soil's stores of soluble nitrogen may also be enriched by the activities of bacteria such as *Azotobacter chroococcum* and *Clos-*

*tridium pasteurianum*. These are universally present in fertile soils and are able to use free gaseous nitrogen to build up their proteins, providing that carbohydrate materials are present and not too much nitrate. If there is an abundance of nitrate they absorb it in preference to the free nitrogen. Nothing is known of the chemistry of this remarkable nitrogen fixation, but it may lead to considerable enrichment of the soil. .

Nitrogen fixation is also carried on by a number of symbiotic bacteria and mycorrhizal fungi (p. 369). The best-known example is *Rhizobium leguminosarum* (*Bacillus radicicola*), which inhabits nodules on the roots of beans (Fig. 228) and other leguminous plants. It exists in the soil as ciliated cocci that multiply upon the surface of the root hairs. The walls become softened and the bacteria enter and penetrate into the cortex which grows out into a nodule. Here the bacteria accumulate as small rods that are sometimes branched in Y and T shapes. They flourish for a time utilising the free nitrogen of the air, but eventually they degenerate and the substance is absorbed by the host. The most notable result of this symbiosis, combined living of two organisms, is the fixation of quite large

amounts of free nitrogen from the soil atmosphere. If the plants rot upon the soil, or are ploughed in, there is an appreciable increase of the soil's store of combined nitrogen with a corresponding increase of fertility. The advantages of growing vetches and clover, both leguminous plants, upon impoverished soil were known to the farmers of classical Greece. The explanation was only discovered at the end of the nineteenth century.

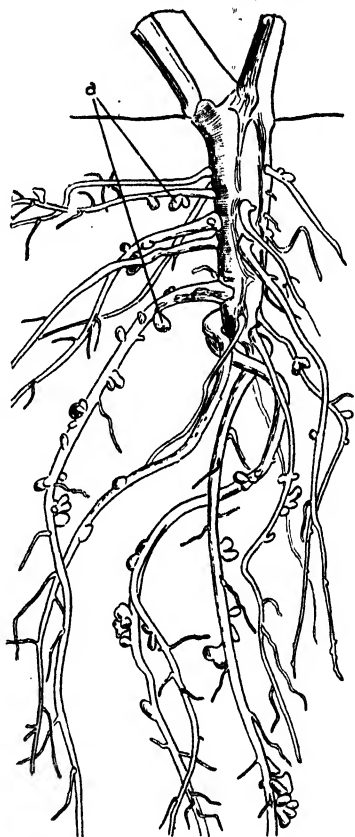


FIG. 228.—Root system of a broad bean plant. *a*, nodules inhabited by nitrogen-fixing bacteria. About nat. size.

The nitrogen cycle supplies a good example of the close and complex ways in which the workings of the organic world are interlocked. Nitrogen is an essential element for all forms of life as we understand it; the action of any one sort of organism if isolated would eventually convert all terrestrial nitrogen into a single end-product that could not be further used. But the end-product of one organism's activity is the starting point of another's. The most various biological processes are involved, fermentation, symbiosis, respira-

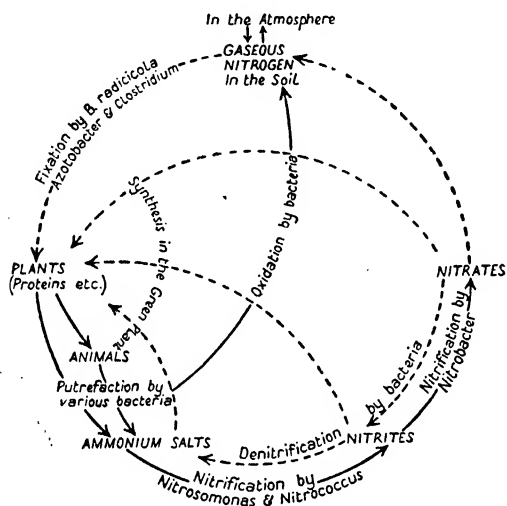


FIG. 229.—The nitrogen cycle. Chemical compounds are shown in capitals, the names of processes in smaller type. The broken lines indicate endergonic reactions (requiring energy), and the continuous lines exergonic reactions (releasing energy).

tion, chemosynthesis, each serving its organism in a different way. The net result is that the cycle as a whole can go on, each organism unwittingly serving the needs of some other. Although the matter of the cycle is in continual circulation, the energy needed for its endergonic reactions (Fig. 229, broken lines) is not. It needs continuous replenishment and this comes from the photosynthesis of the green plant.

A similar cycle of changes could be traced for all the elements entering into biological reactions. Carbon, the most important of all, can be traced through a parallel series of changes to that of nitrogen. The green plant is again the main agent synthesising simple compounds into complex organic ones like carbohydrates and proteins,

which are carbon compounds as well as nitrogenous ones. Chemosynthesis by a variety of bacteria adds its small quota. The agents releasing carbon from complex combinations are the respiration of all types of organisms—plants, animals and bacteria—with the addition of inorganic combustions.

### *Pathogenic Bacteria*

A small proportion of the known bacterial species are partly or wholly parasitic on animals and a quite small number on plants. Partial parasites, such as *Bacillus tetanus* (Fig. 227 E), may live in the soil saprophytically and become parasites on entering the body. Complete parasites, like *Spirochete pallida* (the agent of syphilis, Fig. 227 G) have no life outside the body of the host, and are passed on directly from one person to another. Most infectious diseases are spread in this way. The damage to the host is not usually due to any loss of material caused by the bacteria, but to the production of highly poisonous substances (toxins) in the course of the bacterial metabolism. Diphtheria is caused, for example, through the secretion of toxins in the throat by bacteria lodged there and forming colonies. If the bacteria can be killed before much of the poison has accumulated a cure is effected, but once the toxins are present in quantity, killing the bacteria is useless. Indeed, in the later stages of the disease the bacteria may be already dead, killed by the toxins they have themselves formed. Most hosts produce antitoxins that destroy the toxins of many diseases and so counteract their effect if the attack is not too violent. Vaccination consists of injecting weakened cultures of the disease organism into the human body. This provokes the formation of antitoxins that remain in the body and confer a safeguard against further attacks for a considerable period. The method is successful against smallpox, typhoid, anthrax and other diseases. Antitoxins may also be transferred from the blood of an animal that has recently had the disease into that of another or a human being. This method has proved a successful precaution against diphtheria, tetanus and swine fever.

Pathogenic bacteria are rarely able to penetrate the surface of the body. They gain entrance principally through grazed and cut surfaces. The successful practice of surgery, therefore, depends on an efficient control of the ever-present bacteria. The introduction of antiseptics (p. 352) by Lister resulted in a great decrease in the death rate of surgical patients from blood-poisoning and gangrene. Later, aseptic methods were introduced in which the surgeons' gloves,



instruments and dressings are sterilised beforehand, and the wound is thus kept free from all bacteria. Effective methods in the prevention and cure of human diseases are based upon the detailed study of the nature and activities of the pathogenic bacteria.

#### VIRUSES<sup>1</sup>

In addition to those produced by bacteria there are about a hundred diseases of plants and animals ascribed to viruses. These may be described rather loosely as infective agents that are below the limits of microscopic vision. They cause disturbances in the functions of living cells, and are themselves regenerated in the process. At present viruses are only known as a result of the signs of disease they produce in complex organisms, and nothing can be said about the existence or otherwise of non-parasitic viruses. It is even doubtful whether any viruses have yet been grown artificially in lifeless media, and the great majority certainly require living host cells for their maintenance.

Since viruses are extremely small, they are sometimes called ultrafilterable. This refers to the fact that filters of unglazed porcelain, that will hold back bacteria in a suspending fluid, will not usually retain viruses. The criterion is a very uncertain one, however, and viruses may sometimes fail to penetrate the filters because they are adsorbed on the surface of the pores. Like all other minute bodies they show surface effects very strongly. Some viruses have even been purified from accompanying proteins by successive adsorptions and removals from agents like china clay. The same method can also be used to separate one strain of virus from another.

The degree of organisation possible in a virus is a fascinating problem. Some viruses are very little smaller than bacteria and, in fact, there is no sharp line of division. Among the viruses themselves there appears to be a practically continuous gradation of size down to about 10  $\mu$ . This is very little larger than the starch molecule and we can hardly suppose much organic structure to be possible within such narrow limits as that. It has not unnaturally been suggested that the viruses illustrate the border line between the living and non-living. At the upper end of the series they have attained about the same degree of complexity as the pathogenic bacteria, which they closely resemble in their behaviour. The viruses may increase themselves indefinitely (reproduction), produce symptoms of disease in

<sup>1</sup> Latin *virus*, poison.

their hosts, are killed by the same heat treatment as the vegetative cells of bacteria, and succumb to the same poisons. They are proteins and, at the lower end of the size range, have about the same dimensions as a single protein "molecule." The virus of the mosaic disease of tobacco has been extracted and crystallised. The crystals are rod shaped (Fig. 230), about 500  $\mu\mu$  long and 15  $\mu\mu$  wide with a particle weight of about 17 million. They are stable for long periods and, when reintroduced into the host, develop into the typical active virus again.

### *Bacteriophage*

The bacteriophages are remarkable agencies that appear to fulfil the characteristics of the smallest and least-organised viruses. Like

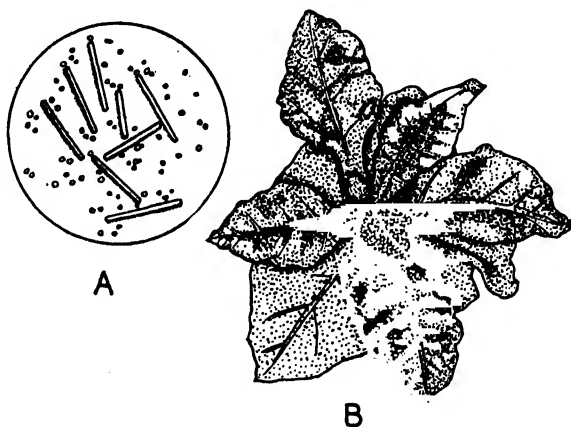


FIG. 230.—Tobacco virus. A, rod-shaped crystals of the virus.  $\times 30,000$ . After Sigurierrsson and Stanley. B, infected tobacco seedling. After Smith.

the similar viruses it is difficult to class them as living or non-living units. Whatever their category in this respect, the effects they produce are so remarkable that their discovery has aroused more interest, perhaps, than anything else in this branch of biology since the discovery of bacteria themselves. Like all the viruses they exist only parasitically, and have never been caused to increase in non-living extracts. They differ from all similar agents however, in the organisms they attack. The viruses in general are all dependent on highly developed plants and animals, but the bacteriophages,<sup>1</sup> as their name implies, attack and destroy bacteria. They were dis-

<sup>1</sup> Greek *phágos* (phagos), eating.

covered independently by two bacteriologists, who found some of their bacterial cultures unexpectedly dissolved away. New and healthy cultures inoculated with a drop of a spoilt one were dissolved away even more rapidly, and this was continued for over a thousand "passages" until the final filtrate, representing only a billionth of a ml. of the original culture, dissolved away 2,000 million bacilli. The bacteriophage, destroying the bacteria and generating and regenerating itself at the same time, may thus be regarded as a living parasite of the bacteria or as an enzyme catalysing its destruction.

*Viruses and Vegetative Propagation. "Loss of Vigour"*

Many plants, when they are reproduced by cuttings or other vegetative means for a number of years, gradually become debilitated. The specimens become poorer and poorer and the crop of flowers, fruit, etc., that they bear becomes less and less. This loss of vigour used to be considered a result of the "unnatural" nature of vegetative propagation and it was said to be one of the biological advantages of sexual reproduction that it invigorated the stock. How the union of two exhausted gametes could produce reinvigoration was never explained, and a much more satisfactory account of the degeneration of vegetatively produced material is now available. The potato plant affords the best illustration of the process, but the explanation can be applied to other species similarly affected; for example, the recent decline in the fertility of strawberry plants is ascribed to the same cause. When infection with a virus disease takes place all parts of the plant are inhabited by the virus, including the young tubers. If these are used for propagation in the usual way, the new plant starts life thoroughly infected and may be still further infected from the soil. Plants do not, like animals, acquire immunity after the first attack but the results of the infections are on the contrary accumulated, and so the successive plants produced from a series of tubers steadily degenerate and after about twenty years are no longer worth cultivation. Virus diseases are much less easily transmitted by seeds, however, so that the great majority of the young seedlings start life entirely free from the disorder, and may be kept perfectly healthy on clean soils. Infected races may even be regenerated by careful selection of the best tubers, and by growing them in suitable districts. The "loss of vigour" is due, therefore, to a definite agent of disease, and not to any inherent deficiency of the potato plant.

**Practical Work**

*All bacteria are extremely small and very careful focusing with the high power is needed to see them.*

(1) **Potato Extract.** Mount a drop of the turbid liquid from the surface of water in which a potato slice has been soaking at 25–30° C. for several days. Put on a coverslip and look for *Bacillus mesentericus*, rod-shaped aerobic bacteria. Draw a drop from the bottom of the water and examine as before. Tapered rods are *Clostridium butyricum*, anaerobic bacteria. Treat both mounts with iodine, note the difference of staining.

(2) **Hay Decoction.** Mount a drop of hot water extract of hay. Observe the delicate rod-shaped *Bacillus subtilis* in motion and often forming chains. The surface layers of the preparation will often show *zooglæa* masses with *spores*.

(3) **Bacterium termo.** Soften a few peas by boiling and allow them to putrify in a small dish of water. Remove some of the scum from the surface and put into a drop of water on a microscope slide. Put on a coverslip, trapping one or two bubbles of air. Examine after a few minutes. Clusters of *Bacterium termo* will be found in violent movement round the bubbles and the edges of the coverslip. Mount a second fragment of scum in freshly boiled and cooled water. Seal with a little vaseline or melted wax round the edges of the coverslip; after about a quarter of an hour the bacteria will come to rest. They are dependent on free oxygen for their activity.

(4) **Root Nodules.** Draw a piece of bean or lupin root showing the nodules. Cut a section through a nodule. Treat with very dilute iodine and mount in dilute glycerine. Make a diagram of the nodule structure showing the *outer parenchyma* with *vascular strands* linking up with those of the root; and the central mass of *cells containing bacteria*.

(5) Crush a portion of a root tubercle in a drop of water on a slide. Cover and examine the characteristic bacteroids (dead bacteria) from the central tissue.

## Chapter XXVIII

### THE FUNGI

The fungi are colourless heterotrophic plants. With few exceptions their bodies are composed of delicate branching threads ramifying through and over their nutrient substrata. The whole system of branching threads is called the mycelium and the individual branches hyphæ.

In their nutrition the fungi may be saprophytic, parasitic or symbiotic, none are autotrophic either by photo- or chemosynthesis. In this respect they resemble the animals, but differ from them in being non-motile, in having walls secreted by their protoplasts and an exceedingly diffuse form of growth. Only dissolved foods can pass into their hyphæ but many of them excrete exo-enzymes (cf. p. 6) that break down solids into soluble forms. The distinction from animals, which secrete similar enzymes into the infolding of their surface called the gut, is in this respect very slight.

Like all other organisms they exist in competition with their neighbours. In the enormously complicated associations of the organic world all degrees of mutual effect exist in uneasy equilibrium. Especially is this true when heterotrophic organisms are considered that must obtain food manufactured by others. Associations are not necessarily fixed and invariable; they may be entirely casual comings together in a crowded world; but out of the medley a relatively few successful combinations emerge, and become noticeable as more or less stable relationships. Terms like symbiosis and parasitism attempt to name some of the more obvious relationships, but as soon as a close examination is made they become subject to fine shades and variations of meaning. *Symbiosis* may be a more or less balanced parasitism, that may be tipped over the precarious edge by a small change of conditions. On the other hand it may create a stable system out of components that could not exist individually. The moulds, *Peronospora* and mycorrhizal types will be described as types of predominantly saprophytic, parasitic and symbiotic fungi respectively.

## SAPROPHYTIC FUNGI: THE MOULDS

The moulds are saprophytic fungi that grow on damp food materials such as bread, jam, cheese and leather. They flourish particularly in damp tropical climates, where it is next to impossible to protect organic materials from them. Their mycelia become visible to the naked eye as white or pink spots on bread, bluish-green streaks on cheese and so on.

*Mucor*

One of the commonest genera of white moulds is *Mucor*. Its mycelium forms a fluffy white felt over the surface of moist bread and many other exposed food materials. Under the microscope it is seen to consist of fine, branched hyphæ (Fig. 231). Each hypha is a non-cellular tube with cytoplasm and numerous nuclei, that are so small that they can only be revealed by special methods of staining. At the centre of the tube is a series of vacuoles, that become smaller towards the rounded growing tip which is almost wholly occupied by cytoplasm. As the hypha grows in length the nuclei at the tip frequently divide.



FIG. 231.—Mycelium of *Mucor* growing in agar. The mycelium has no cross walls and branches freely.  $\times$  about 50.

There are no cross walls in the mycelium and it branches profusely, sending some of its branches into the substratum from which they absorb food substances for the whole. Most *Mucors* are strictly aerobic organisms and do not penetrate deeply into the jam or whatever material they are growing upon. This is fortunate for the housewife, since it means that not more than the surface layer gets spoilt. A few species are capable of anaerobic existence and ferment sugar like yeast. Their hyphæ penetrate more deeply, and they may also bud off single cells; they form alcohol and bubbles of carbon dioxide in the deeper layers.

**Spore Formation.** *Mucor* reproduces most freely by spores. Special hyphæ branch from the mycelium which, unlike its other branches, are negatively geotropic and positively phototropic.

They are borne profusely all over the fertile mycelium, and grow straight up into the air; their tips swell and become filled with dense cytoplasm (Fig. 232 a). Behind the dense tip is a vacuolated zone from which it becomes separated, and in the separation there is secreted a dome-shaped wall, the columella. The dense protoplasm of the tip begins to divide into small fragments each with several

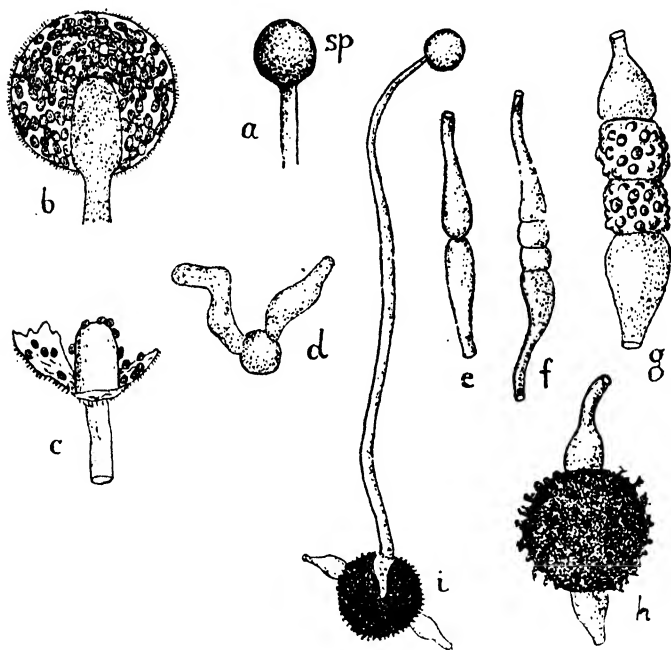


FIG. 232.—Reproduction of *Mucor*. a-c, spore formation; a, young sporangium; b, optical section of mature sporangium; c, columella after dehiscence of the sporangium; d, spore pushing out two germ tubes; e-h, conjugation; e, conjugating hyphæ making contact; f, formation of cross walls; g, wall thickening; h, mature zygote; i, germination of zygote to form a sporangium.

nuclei and, later, a wall. These are the spores. Meanwhile the wall of the swollen tip itself, the sporangium, has become impregnated with calcium oxalate and has turned black. The whole growth, the sporangium and the sporangiophore bearing it, looks like a minute black-headed pin. As the sporangium ripens its frail wall degenerates, and the exposed spores adhering to the columella are slowly dispersed, leaving it naked at the tip (Fig. 232 c). The distribution of the spores by wind and other agencies is very efficient; few exposed surfaces escape them. On a suitable moist substratum they

germinate, pushing out new hyphæ at one or more points (Fig. 232 d). Growth of the mycelium and renewed production of spores may occur under favourable conditions within a few hours.

*Chlamydospore Formation.* In some *Mucor* species the protoplasm may contract into oval masses at short intervals along the hyphæ. Each oval mass secretes a thick wall round itself and may bulge out the wall of the hypha, which eventually breaks up. The released aggregates are called chlamydo—i.e. cloaked—spores on account of their thick walls, in contrast to the spores produced in sporangia whose walls are smooth and thinner. The chlamydospores are resistant, resting forms resembling the spores of bacteria and yeast, and such spores are very common among fungi.

*Conjugation.* Sexual reproduction takes place when tips of two hyphæ arising from the same or different mycelia approach from opposite directions, and come into contact end to end. Each swells into the form of a club (Fig. 232 e), and secretes a cross wall. Where the two tips are in actual contact, the wall is dissolved away, and the protoplasm of the two compartments mingles. The nuclei divide actively and then conjugate in pairs. The wall swells up into a larger dark-coloured sphere with a rough surface. Inside is a thinner wall and the fused protoplasts, forming a single cœnocytic zygote and containing reserve materials, especially fats. The whole structure is 70–80  $\mu$  in diameter, and just visible to the naked eye. It is highly resistant, and capable of remaining inert until conditions are favourable for its germination. On a suitable medium it germinates by rupturing the thick wall, and putting out a hypha which often forms a sporangium at once (Fig. 232 i).

*Heterothallism.* The gametangia of *Mucor*, the tips containing the fusing nuclei, do not show any structural differences and are not separated into distinct sexes. In a few species, and in the closely allied *Rhizopus nigricans*, hyphæ from the same mycelium, even from the same branch, will conjugate and zygotes are freely formed. In most *Mucor* species zygotes are rarer, since conjugation will only occur between hyphæ of different strains. Although they show no visible distinctions, some difference not quite on a par with ordinary sexuality but an interesting parallel to it, must exist between the strains. This functional kind of differentiation is called heterothallism.

#### PARASITIC FUNGI

Some fungi are able to exist either as saprophytes or parasites according to their opportunities. *Mucor* itself may become para-



sitic on young seedlings, which it kills; but it afterwards carries on as a saprophyte upon the plant remains. Such fungi are called *facultative parasites*, but others are *obligate parasites*, being unable to exist (except as resting spores) apart from a living host.

Relatively few fungi are parasitic upon animals. *Saprolegnia* is a facultative parasite upon carp, including goldfish. *Trichophyton* and *Microsporon* species are the cause of ringworm. Their mycelia grow out from a centre, dying away behind and forming the characteristic ring in just the same way that other fungi form fairy rings on a larger scale in grass. *Aspergillus fumigatus* inhabits the lung cavities; while thrush, athlete's foot and a more serious ulceration of the foot common in the tropics are all diseases of fungal origin.

Far more fungi attack plant hosts, causing plant diseases of all kinds and degrees of severity. *Pythium* rapidly damps off the seedlings it attacks and kills them, but the nearly allied fungus *Peronospora* forms a downy mildew that hypertrophies, but does not rapidly kill, the tissues it invades. Among the more destructive fungal parasites are *Hemileia vastatrix* that destroyed the coffee-planting industry of Ceylon in the eighteen-seventies and *Phytophthora infestans*, the cause of potato and tomato blight. On its first arrival in Europe in the eighteen-forties it caused the great Irish potato famine that necessitated the repeal of the Corn Laws. In any rainy summer it is likely to appear in the damp south-west of Ireland and in Cornwall as early as the end of May. Thence it spreads north-eastwards as the conidia, similar to those of *Peronospora* (p. 368), are borne on the prevailing south-west winds. It usually appears in the great potato-growing districts of Cambridge and Lincolnshire in late July or early August. A warm, moist atmosphere with frequent south-westerlies are the conditions most favourable to its development; in dry summers its effects are usually negligible. The cereal rusts, *Puccinia* spp., take a heavy yearly toll of cereal crops all over the world. They do not destroy the plants, but enfeeble them, and reduce their growth and grain production by a heavy percentage.

### *Methods of Control*

The fungal diseases of plants can rarely be cured, and methods of control aim at preventing or mitigating the attacks. They have to be based on a knowledge of the nature and life history both of the parasite and of the host. Methods of plant hygiene, such as correct spacing, avoidance of infected soils by rotation of crops, good

aeration and fertility of the soil, contribute to the production of healthy plants resistant to fungal attack.

Preventive spraying at a suitable or vulnerable stage of the plant's development is also a major resource. The principle of the method is to cover the plant with a fungal poison, and so kill the wind-borne spores as they germinate upon its surface. Potato blight (*Phytophthora*) is controlled by spraying the haulms with Bordeaux mixture, a colloidal solution of copper sulphate and lime. The colloidal particles do not penetrate the cuticle and poison the plant tissues, but are lethal to fungal hyphæ.

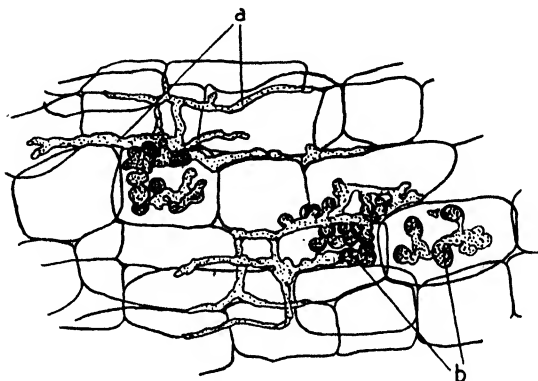


FIG. 233.—*Peronospora* in the pith of *Capsella bursa-pastoris*. *a*, mycelium in intercellular spaces; *b*, haustoria inside the cells.  $\times 100$ .

Soil infections are more difficult to deal with. Sterilisation by steam heat is practicable on relatively small areas, such as the soil of tomato greenhouses. Liming prevents diseases such as finger-and-toe disease of Brassicas (*Plasmodiophora brassicae*); but the most important long-term policy is the breeding of disease-resistant varieties.

### *Peronospora*

*Peronospora* is an example of an obligate parasite of relatively simple structure and life history. There are numerous species, each of which attacks a particular host species. Altogether they form "downy mildews" on a wide range of host plants including such economically important ones as onions, clover, mangolds, cabbages, tobacco and maize.

The mycelium consists of long-branching hyphæ that spread through the continuous intercellular-space system of the host plant,

especially in the stem. The long hyphæ do not enter the host cells, but send off short lateral hyphæ, which do penetrate into them and branch freely, more or less filling the cell cavity and absorbing the contents (Fig. 233b). These *haustoria* are very characteristic of *Peronospora*.

*Asexual Reproduction.* The mycelium sends out branches called conidiophores, that grow out through the stomata into the open air. They project for a fraction of a millimetre, and are produced in vast numbers so that the surface of the leaf or stem takes on a soft downy appearance. The colour is white or off-white. Outside the host tissues

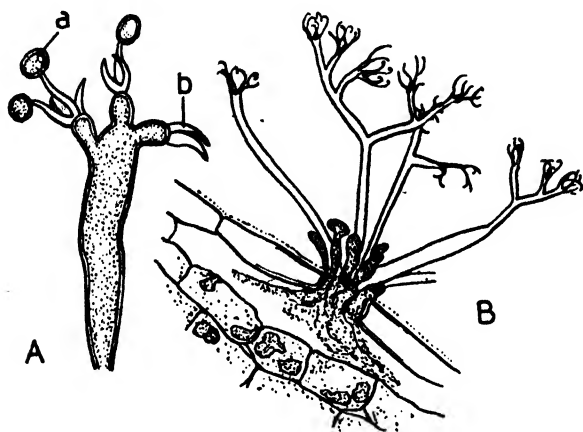


FIG. 234.—*Peronospora* conidia. A, single conidiophore; a, conidium; b, branchlet after shedding conidium. B, bunch of conidiophores extruded through a stoma. All conidia have been shed.  $\times 130$ .

the conidiophores bifurcate freely, and at the end of each branchlet an ovoid swelling is produced with nuclei and attendant cytoplasm. This swelling, a conidium, becomes much larger than its hypha and is eventually attached only by a narrow constriction (Fig. 234). This is severed at the slightest pretext, and the conidium is blown away upon the wind.

This method of producing conidia has obvious similarities with the method of sporangium production in *Mucor*. The conidium does not divide up into spores but is distributed as a whole. Like the spores of *Mucor* conidia are produced in vast numbers, and spread the fungus far and wide. They are subject to the same chances as wind-borne pollen and only a minute fraction of the conidia disseminated alight on a suitable spot for germination. Those that

alight upon the surface of a suitable host sprout a hyphal tube, which enters by way of a stoma and starts a new mycelium.

**Sexual Reproduction.** Sexual reproduction occurs at a late stage when food supplies are becoming scarce in the impoverished tissues of the host. Gametangia are formed, as in *Mucor*, but they are sexually differentiated both in size and activity. The female organ is formed deep inside the host tissues by the swelling of the end of a hypha into a spherical *oogonium* that is cut off by a wall (Fig. 235 a). Just behind the oogonium a lateral branch develops and grows up to the side of the oogonium; it is also cut off by a wall and is the *antheridium*. Both gametangia have numerous nuclei at first, but all save one degenerate in each. When they are ready for fertilisation there is a single egg nucleus in the oogonium and a single male nucleus in the antheridium. Conjugation takes place through a narrow tube that grows out from the antheridium into the oogonium. The male nucleus and some cytoplasm pass through the tube into the oogonium where the two nuclei fuse. The resulting zygote secretes a thick resistant wall, and lies dormant as the host tissues rot away around it. It may remain in the soil for months and ultimately germinate when conditions are favourable.

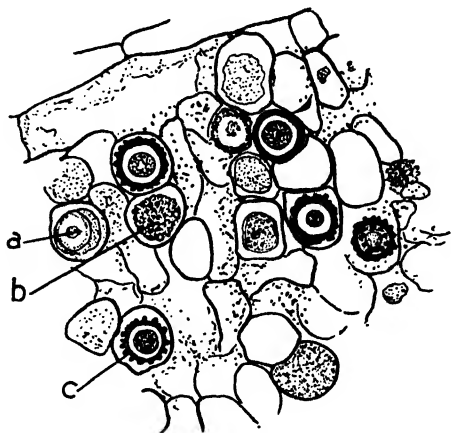


FIG. 235.—*Peronospora* oospores in cortex of *Capsella bursa-pastoris*. a, oogonium ready for fertilisation; b, zygote in surface view; c, zygote in sectional view.  $\times 130$ .

#### SYMBIOTIC FUNGI: MYCORRHIZAS

The surface tissues of roots and the dead outer layers they are constantly sloughing off are colonised by numerous soil organisms including bacteria and fungi. Some of them are mildly parasitic, and some form characteristic associations like the nodule bacteria with the *Leguminosæ* (p. 355). Consistent relations of fungi with roots lead to the formation of associations called mycorrhizas. These are morphologically of two kinds, *ectotrophic* in which the

fungal mycelium forms a mantle over the surface of the root and in the intercellular spaces but rarely penetrates into its cells; and *endotrophic* where there is little or no fungal mantle, but various sorts of filtration into the cells, though usually not beyond the cortex. Mycorrhizas of one or the other type are extremely common among the Angiosperms and are found among the Gymnosperms and Pteridophytes also. The simpler land plants, the gametophytes of Pteridophytes and Bryophytes, also form symbiotic associations with fungi, while algæ form the very close associations called the Lichens.

#### *Ectotrophic Mycorrhiza of Pinus*

The roots of *Pinus* and other related trees form ectotrophic mycorrhizas with numerous toadstool fungi of the genera *Boletus*, *Lactarius*, *Scleroderma* and others. Infection is limited to the root systems. In acid, peaty soils, and other soils with large amounts of raw humus, the development of the trees is very poor if no mycorrhiza-forming fungus is present. There is considerable evidence that healthy growth depends on mycorrhizal infection from an early seedling stage, though germination itself occurs without it. An even greater dependence on mycorrhiza is shown by the seeds of orchids that lie in a partly developed and dormant state in the soil until infection with the appropriate fungus, usually a *Rhizoctonia* sp., happens to occur. Although the fungi associated with *Pinus* behave as saprophytes, they make very slow growth on the complicated organic compounds present in raw humus. They grow much more satisfactorily if free sugar is provided together with the vitamins aneurin and biotin. It is suggested that in the mycorrhizal association they obtain these necessities from the root tissues, and so are enabled to compete with the other soil organisms for nitrogenous and general soil nutrients. Some of the nutrients find their way into the root tissues, which would otherwise fail to obtain them under the acid soil conditions unfavourable to nitrification and root growth. The symbiosis of the pines and the toadstool fungi appears to result in a system which can exist and flourish in a situation that neither partner could colonise alone. The planting of properly infected seedlings has made it possible to raise soft-wood plantations on wide areas of waste land where all previous attempts had failed.

#### *Endotrophic Mycorrhiza of Calluna*

The heather plant, *Calluna*, also dominates wide areas of poor acid soils with a very low content of available nitrogen. It is enabled

to do so by its association with the fungus *Phoma*. The mycorrhiza they form is endotrophic and the fungal hyphæ extend into all parts of the plant, including even the ovary and the testa of the seed. They are most abundant in the root cortex. The mycorrhizal fungi in orchid roots are strictly limited to the outer cortex (Fig. 236) and the

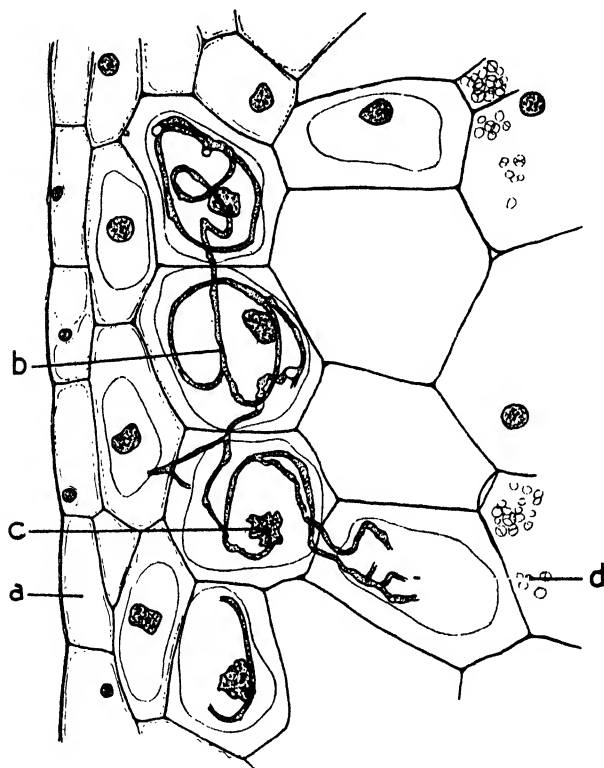


FIG. 236.—Endotrophic mycorrhiza in cortex of *Neottia nidus-avis*. *a*, epidermis; *b*, fungal hypha; *c*, nucleus; *d*, deeper-seated cell in which fungus is becoming digested. Drawing by J. W. Wilson.

inner cortical cells produce a substance capable of dissolving its hyphæ. No such substance seems to be formed by *Calluna*, and the fungus penetrates into all parts of the host body. Infection usually takes place during the early stages of germination, and the fungus enters the young host cells. In the absence of the fungus germination fails. *Phoma* possesses the power of fixing free nitrogen, and so has an added advantage over the mycorrhiza of *Pinus*. The *Calluna*-

*Phoma* combination is very successful in acid soils, which are not only poor in available nitrogen but also poor in nitrogen-fixing and nitrifying bacteria. It is therefore easy to understand the success of *Calluna* and the related *Ericas*, similarly infected, in competition with other plants on peaty moors and heaths.

### *Vitamins*

Vitamins are complex organic substances that are required in minute amounts for normal growth. The vitamins known at the present time are very various both in their chemical compositions and in their functions. They have mostly been discovered through the diseases of animals caused by an absence or deficiency of them in the diet. The absence of Vitamin C from the crudely preserved stores of the old sailing ships was the cause of scurvy and the reason for carrying fresh lime juice, rich in this vitamin. Such diseases happen because the animal organism needs the vitamins and is itself unable to synthesise them. Green plants are the source of the vitamins and, although some at least are needed by their metabolism, vitamin-deficiency diseases are not so obvious among them. The synthesis of Vitamin B (aneurin, thiamin), appears to take place in the shoot, since the growth of isolated tomato roots can be much prolonged by its addition, with sugar, to the culture solution. The fungi and bacteria are very diverse in their vitamin requirements, usually being able to synthesise some themselves and requiring to get others from their food (see *Pinus mycorrhiza* above). The functions of the vitamins are not always known, but some are co-enzymes. Vitamin B becomes cocarboxylase (p. 83) in the living cell, and Vitamin C (ascorbic acid) is an important hydrogen carrier (p. 89) in plant oxidising systems.

### *Antibiotics*

Many organisms produce substances that are poisonous to others though not poisonous to themselves. Thus the quinine that accumulates in large quantities in the bark of the *Cinchona* tree is very poisonous to the parasitic protozoa that are the cause of malaria. It is improbable that the *Cinchona* tree itself derives any special advantage, not being vulnerable to such attacks. The poison produced by the inner cortex of orchid roots (p. 371), on the other hand, has a notable effect in controlling the growth of invading mycorrhizal fungi. The seeds of radish (*Raphanus sativus*) produce a substance, raphanin, that inhibits the germination of other species in a concen-

tration of 1 in 10,000 though the radish seedlings themselves are not affected even at much higher concentrations. Such substances appear to be produced by many seeds. Raphanin also stops the growth of various bacteria. Bactericidal antibiotics are also known to be formed by moulds, green algæ, actinomycetes (Protista) and *Bacillus brevis*. The most famous of these substances is penicillin, formed by the green mould *Penicillium*

*notatum*. It is exceedingly toxic to many bacteria, and will stop their growth in concentrations as low as one in a million. It was discovered by its effect upon a culture of staphylococci that accidentally became contaminated with *P. notatum*. Penicillin diffuses out from the mould so that an area free of bacteria exists all round it (Fig. 237). Penicillin owes its special importance to two other factors besides its great activity; many of the bacteria it attacks are agents of the

most serious human diseases and, in spite of its great toxicity to bacteria, it is not poisonous to human beings even in relatively large doses. It has proved to be the ideal agent for healing infected wounds and stopping some deeper-seated bacterial infections. It is produced on a commercial scale by vast cultures of the mould.

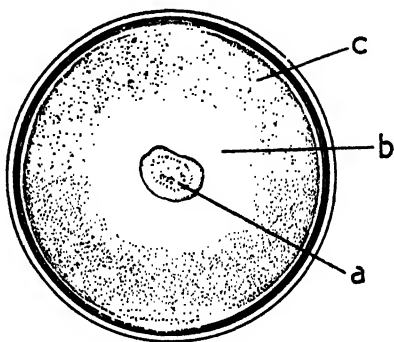


FIG. 237.—a, culture of *Penicillium notatum* on nutrient agar; b, sterilised area; c, cloudy area infested with *Staphylococci*. From a photograph by Chain and Florey.

## Practical Work

### SAPROPHYTIC FUNGI

(1) Examine a culture of *Mucor hiemalis* (or other species) first with a hand lens and then with the low power. This can be done through the lid if the culture is in a Petri dish. Invert and look for hyphæ growing in the solid medium. Draw a small part of the mycelium showing upright *sporangiophores* and *sporangia*.

(2) Cut out a small part of the agar jelly with its mycelium and cover the dish again immediately. Put a very small portion on a slide and add a drop of alcohol, to remove air, followed immediately by a drop of water. Allow the jelly to soften and then put on a coverslip and squeeze gently. Irrigate with iodine solution and examine under the high power. Draw a hypha showing *tip* filled with protoplasm, thin walls, lining of *protoplasm*, large *vacuole*. Nuclei are too small to be seen. Draw a *sporangiophore* with young *sporangium*, showing *columella*, dense outer



*cytoplasm* or *spores* and an old dehiscent sporangium consisting of the columella with a few attached spores.

(3) Examine a culture-plate sown with + and - strains of *Mucor hiemalis* (heterothallic). Note that the *zygospores* are formed only where the different strains meet. Remove a small portion of agar from the line of contact. Mount as in (2) and examine for stages of conjugation.

*Note.* If pure cultures of *Mucor* are not available, good material for examination can be obtained by moistening a piece of bread, wiping it over the floor and keeping it under a moist bell-jar in a warm place for a few days. *Mucor* will be well represented in the resulting mixture of moulds.

#### PARASITIC FUNGI

(4) Examine specimens of *Capsella* or other cruciferous species attacked by *Peronospora*, and observe the gall-like distortions.

(5) Examine the infected surface under the microscope and draw a branched *conidlophore* protruding from a stoma, with its *conidia*.

(6) Mount a longitudinal section of an infected stem and irrigate with iodine, watching as the iodine penetrates. Note and draw non-septate *hyphæ* running between host cells, and short, branched *haustoria* within the cells. Look for the nucleus. Look also for special *oögonia*, club-shaped *antheridia* and rough-walled *zygotes*.

## SPECIAL REAGENTS

- Aniline Chloride (or Sulphate).* Make up a saturated solution in water, filter and acidify with a few drops of hydrochloric acid.
- Baryta Water.* Dissolve about 50 gm. barium hydroxide and 15 gm. barium chloride in 500 ml. boiling distilled water. Allow to cool under soda lime. Excess barium hydroxide will crystallise out and the clear solution may be drawn off as required.
- Chloral Hydrate.* Dissolve 160 gm. chloral hydrate crystals in 100 ml. distilled water.
- Chlor-zinc-iodine (Schulze's solution).* Dissolve 110 gm. zinc in 300 ml. concentrated hydrochloric acid, and evaporate to half the volume. Add a little extra zinc during evaporation to make sure that all acid is neutralised. Dissolve 10 gm. potassium iodide in the least possible amount of water and add 0.15 gm. iodine. Mix the two solutions and filter through glass wool if turbid. Keep in a tightly stoppered bottle in the dark.
- Chromic Acid, 5 per cent.* Dissolve 6.5 gm. potassium bichromate in about 75 ml. water and cautiously add 2.2 gm. concentrated sulphuric acid. When cool make up to 100 ml.
- Fehling's Solution.* A.—7 gm. crystalline copper sulphate in 100 ml. water. B.—35 gm. Rochelle salt (sodium potassium tartrate) and 10 gm. caustic soda in 100 ml. water. Mix equal quantities of A and B immediately before use.
- Glycerine (dilute solution).* Make up 5 gm. pure glycerine to 100 ml. with distilled water.
- Iodine Solution.* Make a strong solution of potassium iodide. Add some crystals of iodine and shake. The solution should be a deep golden brown.
- Iodine Tincture.* Shake up iodine crystals with alcohol until a deep golden brown solution is obtained.
- Lead Acetate.* Dissolve 10 gm. lead acetate in water and make up to 100 ml. Filter and keep in a well-stoppered bottle.
- Lime Water.* Shake up an excess of freshly slaked lime with distilled water in a Winchester. Allow to stand until clear and then siphon off the clear liquid as required. Can be obtained from druggists.
- Millon's Reagent.* Dissolve 15 gm. mercury in 43 ml. concentrated nitric acid in a fume cupboard. Dilute with 80 ml. distilled water and filter after 2 hours. Can be obtained from dealers.
- Phloroglucinol.* Make a saturated solution in alcohol and gradually add strong hydrochloric acid until precipitation begins.
- Sodium Cobaltinitrite.* Dissolve 20 gm. cobalt nitrate, 35 gm. sodium nitrite in 65 ml. water and 10 ml. glacial acetic acid. Filter, if necessary, and keep in a cool place.
- Sudan III and Sudan IV.* Saturated solutions in 70 per cent. alcohol. Sudan III is the more stable.
- Trichloroacetic Acid.* Dissolve 10 gm. crystals and make up to 100 ml. with distilled water.

# INDEX

Principal entries are in bold type : italic numerals indicate that a text figure is included.

- Abies magnifica*, 11  
 abscission layer, 276, 285  
 absorption, band, 65  
     of salts, 255  
     of water, 253  
*Acacia*, 335  
*Acacia pycnantha*, 336  
*Acer pseudoplatanus*, 260, 266-272  
 acetaldehyde, 83, 90  
 acetic acid, 350  
 achene, 307, 310, 311, 319  
 acorn, 315  
 adaptability, 354  
 adaptation, 121, 135, 158, 339  
*Adiantum cuneatum*, 12  
*Adiantum reniforme*, 12  
 adsorption, 35  
*Aesculus hippocastanus*, 260  
 after-ripening, 315  
 agar, 86, 210  
*Agropyrum repens*, 185  
 albumin, 80  
 alcohol, 33, 36, 37, 88, 90, 342  
 alcoholic fermentation, 90, 342  
 aleurone cell, 81  
     grain, 81  
 Algæ, 13, 43  
     brown, 124-137  
     green, 95-122  
     red, 124  
 alkaloid, 81  
 allelomorph pair, 325-330, 338  
 almond, 309  
 alternation of generations, 140, 148-151, 158  
 alveoli, 18  
 amino-acid, 80, 86, 227, 316  
 ammonia, 86, 354  
 ammonium, 256  
     carbonate, 354  
     sulphate, 353  
     tartrate, 341  
*Amæba*, 17-21, 28, 41  
     contractile vacuole, 20  
     encystment, 21  
     excretion, 19  
     growth, 21  
     irritability, 20  
     movement, 18  
     nutrition, 19  
     reproduction, 20  
     structure, 17  
*Amæba limax*, 17, 18, 19, 20  
*Amæba proteus*, 17, 35  
 amylase, 77, 88, 316  
 amyloid, 79  
 amylopectin, 77  
 anabolism, 85, 92  
 anaerobe, 349  
 anaphase, 55, 333  
 andrœcium, 295, 298  
 angiosperm, 11, 168, 177, 178-322, 335  
 Angstrom unit, 32, 34  
 animal, 1, 3, 69, 321  
     cell, 28, 43, 45  
     colonial, 6  
     diseases, 357  
     energy, 7, 92  
     food, 7  
     nitrogen cycle, 356  
     nomenclature, 9  
     organisation, 4  
     seed dispersal by, 312  
     soma, 112  
     unicellular, 17  
 anisogamete, 104  
 anisogamy, 102, 122  
 annual, 178, 181, 233, 281, 283  
 annual ring, 269  
 annulus, 154  
 anther, 296-300  
 antheridial cell, 170  
 antheridium, 111, 133, 142, 156, 157, 369  
 antibiotic, 372  
 antipodal, 301  
*Antirrhinum*, 309, 330  
 antiseptic, 352, 357  
 antitoxin, 357  
 apple, 277, 315  
     spur, 262  
     tree, 264, 282  
 archegonium, 143, 156, 158, 166, 173  
 ascorbic acid, 89  
     oxidase, 89, 257  
 ash, 312  
 asparagine, 353  
*Asparagus*, 186  
*Asplenium*, 194  
 assimilation, 2, 21, 44  
 aster, 51  
 auxin, 284, 289  
 axil, 182, 186, 191, 193, 217, 223  
 axillary bud, 181-192  
*Azotobacter*, 354, 356  
 bacillus, 347  
*Bacillus anthracis*, 351  
*Bacillus radicularis*, 355  
*Bacillus tetanus*, 347, 348, 357

- bacteria, 13, 19, 346-358
  - capsule, 346
  - chemosynthetic, 348
  - dispersal, 351
  - fermentations, 350
  - movements, 340
  - nitrifying, 354
  - parasitic, 348
  - pathogenic, 357
  - photosynthetic, 347
  - pure cultures, 352
  - putrefactive, 353
  - reproduction, 350
  - respiration, 349
  - saprophytic, 348
  - size, 346
  - species, 353
  - strains, 353
  - structure, 340
  - symbiotic, 355
- bacteriochlorophyll, 347
- bacteriophage, 35, 359
- Bacterium aceticum*, 350
- Bacterium acidipropionici*, 349
- Bacterium coli mutabile*, 353
- bamboo, 239
- bark, 3, 274
- barley, 320
  - grains, 344
- bean, 289, 304, 307, 317
  - root nodules, 355
  - seedling, 319
- bee, 296
- beech, 246, 282
- beef-steak plant, 321
- beet, 179, 198, 199
- beetroot, 279
- Beggiatoa*, 348
- belladonna, 180, 198, 222, 313
- berry, 308, 313
- Betula alba*, 261, 275
- biennial, 179
- binary fission, 21, 350
- birch, 261, 275
- birds, 312, 321
- bivalent, 332, 333
- blackberry, 8
- Bordeaux mixture, 367
- boron, 257
- bracken, 160, 185
- bract, 261-263, 295
- bramble, 183
- branch, 181, 260, 277, 288
- branching, 245
- bread making, 344
- breathing, 88
- breeding, 336
- brewing, 344
- broom, 308
- Brown, Robert, 46
- Brownian movement, 33, 34, 42
- Bryophyta, 12
- bud, 2, 181-191, 213, 216, 284
  - adventitious, 180
  - lateral, 260, 262-264, 284
  - scale, 223
  - terminal, 260, 262, 264, 283
- budding, 343
- bulb, 191, 262
- bulbil, 190, 192
- bunchy-top, 260
- bundle sheath, 225, 226
- bush, 261
- buttercup, corm, 189
  - flower, 294-297, 334
  - fruit, 307
  - inflorescence, 292
  - order, 10
  - runners, 183
- Cactaceae, 324
- cactus, 5, 229
- calcium, 42, 256
  - oxalate, 364
  - pectate, 248, 276
- Calluna mycorrhiza*, 370
- callus, 202
- calyx, 295, 311
- cambial stimulus, 285
- cambium, 236, 265-267, 278
  - wound, 267
- cane sugar, 38, 76
- Canna*, 317
- capsule, 308, 309, 321
- carbohydrates, 26, 46, 73-78, 86, 283
- carbon, 69, 72
  - atom, 69, 72
  - cycle, 69, 366
- carbon-dioxide, 85
  - chemosynthetic, 348, 354
  - fermentation, 342
  - narcotic, 315
  - photosynthetic, 4, 64, 67-69, 127, 347
  - respiratory, 20, 46, 88-92
- carbonate, 67, 69
- carboxylase, 83, 87, 316, 342
- carotin, 124
- carpel, 182, 295, 296-298, 300, 307-310
- carrot, 179, 198, 257
- Casparian strip, 250
- castor-oil seed, 317, 318
- catalyst, 82, 89
- catkin, 292, 293, 299
- cedar, 11, 168
- cell, 3, 21, 41-61
  - animal, 28, 43, 45, 56
  - apical, 131, 135, 141, 146, 155
  - companion, 201, 225, 237, 241, 251, 268
  - conducting, 200-206
  - division, 56, 116, 343
  - doctrine, 42-44
  - epidermal, 50

- cell (*continued*)  
 germ, 97, 139  
 glandular, 197  
 green, 64-68, 88  
 mechanical, 202, 206  
 passage, 253  
 pith, 218  
 plant, 46-48  
 sap, 57  
 secretory, 197  
 shape, 215  
 storage, 198, 199  
 structure, 3, 46  
 surface, 199, 210, 256  
 wall, 3, 21, 44, 56, 99, 204-210, 271  
 water relations, 58-61
- cellobiose, 78  
 cellulose, 46, 57, 77, 86, 206, 248, 273  
 centromere, 51, 332  
 centrosome, 53  
 cereal, 319-321  
 charcoal, 82  
 charge, 33  
 cheese making, 350  
 chemical constitution, 6  
 chemosynthesis, 348, 354  
 chemotaxis, 286, 347  
 chiasma, 332  
   formation, 333  
 chitin, 29  
*Chlamydomonas*, 6, 13, 28, 35, 97-103,  
   114, 121  
   nutrition, 99  
   reproduction, 100  
   sex differentiation, 102  
   structure, 97, 98  
*Chlamydomonas braunii*, 102, 122  
*Chlamydomonas coccifera*, 122  
 chlamydospore, 365  
 chlorophyll, 4, 13, 64-68, 124, 256, 331  
   formation, 338  
 chloroplast, 22, 64-68, 98, 113, 116,  
   141, 162, 226, 286  
 chlorosis, 257  
 chromatid, 51, 332  
 chromatin strands, 341  
 chromomere, 332  
 chromoprotein, 81  
 chromosome, 49, 51-56, 148, 175, 304,  
   331-334  
 cilium, 346  
*Cinchona*, 372  
 classification, 7  
 clay, 31, 35  
 clone, 192, 324  
*Clostridium*, 349, 354, 356  
 clubmoss, 12, 160  
 coagulation, 42  
 coal measures, 12  
 coccus, 35, 346, 355  
 coconut, 313  
 cænobium, 96, 103, 106, 108  
 cænocyte, 43  
 oo-enzyme, 82, 372  
*Colchicum autumnale*, 190  
 cold, 282, 315  
 coleoptile, 284, 289, 320  
 collenchyma, 206, 225, 234, 243  
 colloid, 31, 38  
 colloidal dimension, 33, 35  
   particles, 33  
 colony, 103, 105, 107, 109, 353  
 colour, 326  
 columella, 364  
 competition, 321  
 concentration gradient, 21  
 conceptacle, 126, 130  
 conduction, 204  
 cone, 11, 160, 163, 169, 171  
 cone scale, 11, 176  
 congo red, 34  
 conidiophore, 368  
 conidium, 368  
 conjugation, 101, 104, 117, 121, 364,  
   369  
   canal, 118, 121  
*Convolvulus arvensis*, 184  
 copper, 257  
 coral, 6  
 cork, 46, 210, 266, 273-278  
 corm, 188-190  
 corolla, 295  
 correlation, 283  
 correlative inhibition, 284  
 cortex, 126, 233-235, 250, 253, 273,  
   371  
 cotton, 78, 209  
 cotyledon, 176, 182, 304, 306, 309,  
   316-320  
*Craterellus cornucopioides*, 14  
*Crocus*, 189  
 crossing, 326-331  
 crystalloid, 31, 38  
 cuticle, 69, 200, 215, 223, 227, 234, 335,  
   367  
 cutin, 79, 200, 210  
 cutinisation, 210  
 cutting, 284  
 cyanide, 19, 24, 90, 256  
 cyme, 292, 294, 297  
 cypress, 168, 260, 335  
 cyst, 21  
 cytoplasm, 41, 98, 115, 200, 341,  
   363  
 cytoplasmic bridle, 48, 127  
   fibril, 108  
 dandelion, 181  
 Darwin, 14, 336  
*Datura stramonium*, 313  
 day-length, 282  
 death rate, 321  
 defæcation, 19  
 deficiency signs, 257

- dehydrogenase, 82, 83, 89
- Delphinium*, 308, 334
- dermatogen, 215, 246
- desiccation, 21, 193
- desmogen, 218
- desmolase, 83
- development, 282
- dextrin, 77
- diakinesis, 332
- dialysis, 38
- diatom, 17
- dicotyledon, 182, 243, 265
- Dictyota*, 149
- Dictyota dichotoma*, 151
- differentiation, 6, 124, 141, 219
- diffusion, 38, 67, 230, 256
- digestion, 88, 91, 316
- diplotene, 332
- disaccharide, 74, 76
- disease, 14, 348
  - bacterial, 357
  - fungal, 366
  - virus, 358
  - vitamin deficiency, 372
- dispersal, 310-313, 351
- distilling, 344
- distribution, 336
  - cysts, 21
- dog rose, 9
- dominance, 327
- dormancy, 2, 315
- downy mildew, 367
- Drosera rotundifolia*, 5
- drupe, 308, 310
- dry weight, 281
- Dryopteris*, 149-159, 202
- dye, 36
  
- ebony, 272
- ectoplasm, 18, 20, 48
- edestin, 79
- egg, 41, 107, 111, 120, 132, 144, 150, 157, 161, 175, 301, 369
- elater, 146
- elder, 260
- electrolyte, 33
- electron, 34
- elm, 260, 275
- elongation, 247, 284
- embryo, 134, 135, 144, 157, 158, 166, 175, 304, 306, 313, 316
  - sac, 301-304
- embryology, 335
- emulsion, 32, 79
- emulsoid, 32
- encystment, 21, 27
- endocarp, 310
- endodermis, 250, 253, 278
- endoplasm, 18, 20, 48, 57
- endosperm, 176, 304, 306, 316-320
- energy, 1, 7, 68-69, 85, 92, 254
  - electrochemical, 7, 348
- energy (continued)
  - free, 7
  - nitrogen cycle, 356
  - radiant, 7
- enzyme, 19, 41, 81-83, 88, 256, 345
  - block, 87
  - formation, 316
- epicarp, 310
- epicotyl, 319
- epidermis, 215, 226-229, 233, 273
- Equisetum arvense*, 12, 160
- erect position, 242
- ester, 75, 92
- Eudorina*, 35, 105-108
  - reproduction, 106
- Eudorina elegans*, 105, 106
- Eudorina illinoiensis*, 105, 106
- Eudorina indica*, 105, 106
- Euglena*, 13, 22-28, 35, 41, 65
  - contractile vacuole, 27
  - encystment, 27
  - excretion, 26
  - irritability, 27
  - movement, 23
  - nutrition, 26
  - reproduction, 27
  - structure, 23
- Euglena gracilis*, 25
- Euglena viridis*, 23
- Euplotes*, 29
- Euryale ferox*, 42
- evaporation, 154, 229
- evening primrose, 287, 338
- evergreen, 168, 261
  - tree, 11
- evolution, 14, 121, 334-339
  - evidence, 334
  - method, 337
- excretion, 20, 21, 22, 26
- exo-enzyme, 362
- eye spot, 27, 99, 100, 103, 108
  
- fæces, 19
- family, 9
- fat, 78, 81, 102, 118, 316, 321
  - droplets, 36
  - globules, 19, 32
  - respiration, 91
- fatty acid, 210
- feeding habits, 3
- Fehling's test, 75
- fermentation, 69, 90, 350
  - alcoholic, 342, 344
- fern, 12, 160
- fertilisation, 144, 157, 165, 174, 175, 301-304, 369
- fibre, 129, 202, 206, 240, 243, 267-270, 299
  - bundle sheath, 242
  - pericycle, 236, 267
  - phloem, 267
  - substitute, 267, 270

- figwort, 322  
 filament, algal, 95, 113–118, 155  
   floral, 296, 298  
 filtration sterilisation, 352  
 fir, 11, 168  
 fitness, 339  
 fixation, 42, 51  
 flagellum, 23–26, 98, 103, 105, 108, 114,  
   142, 156, 346  
 floral diagram, 296  
 floral structure, 10, 294–298  
 flower, 11, 182, 287, 288, 292–304, 326  
   bud, 181, 295  
   formation, 282  
   movements, 287  
 flowering, 282  
   hormone, 282  
   plant, 11, 178 *et seq.*  
 foam, 32  
 fog, 32  
 follicle, 308  
 food, 7, 20, 85, 192, 320  
   reserve, 282  
   storage, 181  
   vacuole, 19  
 foot, 157  
 form, 4, 6, 11  
 fossil record, 335  
 frond, 12, 125, 126, 136, 151, 152  
 fructose, 68, 74, 88  
 fruit, 8, 182, 279, 289, 307–313  
   abscission layers, 277  
   dry, 307  
   fleshy, 264, 285, 308  
   formation, 282, 307  
   growth, 281  
   sugar, 74  
   unripe, 91  
 fucoxanthin, 124  
*Fucus*, 13, 41, 46, 97, 124–137, 149  
   development, 135  
   nutrition, 129  
   reproduction, 130–135  
   structure, 126–129  
*Fucus serratus*, 125, 130, 131  
*Fucus spiralis*, 125, 130  
*Fucus vesiculosus*, 125, 131, 134  
 function, 4, 6, 44, 121  
 Fungi, 13, 14, 43, 340, 362–373  
  
 gametangium, 365, 369  
 gamete, 101–118, 121, 130, 141, 150,  
   301, 325–328  
   potential, 343  
 gametophyte, 150, 155, 164, 165, 170,  
   173  
 gas, 3  
 gaseous exchange, 2  
 gel, 36  
   membrane, 18, 41  
 gelatine, 32, 33, 37, 42  
 gemmæ, 13, 193  
  
 gene, 325–334, 338  
 genetics, 325–334  
 genotype, 122, 337  
 genus, 9  
 geotropism, 288  
 germination, 92, 282, 315–320  
   inhibition of, 372  
*Ginkgo biloba*, 168  
 gland, 197  
 glandular cell, 198, 261  
 glandular hair, 198  
 globulin, 80  
 glucose, 35, 68, 74, 88  
 glucose-1-phosphate, 77  
 glue, 31  
 glutelin, 81  
 glycerol, 79  
 glycine, 80  
 glycogen, 7, 78, 341  
 glycolysis, 86, 89, 90  
 glycoside, 75  
 gold, 33–35  
*Gonium pectorale*, 96  
 gooseberry, 309  
 Graham, 38  
 grain, barley, 81, 316  
   cereal, 81, 313  
   ship, 37  
   silver, 280  
   starch, 76  
 grana, 65, 66  
 grape, 344  
 grasses, 321  
 gravity, 288  
*Gromia*, 29  
 ground-nut, 321  
 growing point, 213–219, 245–247, 284,  
   316  
 growth, 2, 21, 230, 260, 266, 281–285,  
   342  
   cycle, 281  
   hormone, 284  
   rate, 281, 284  
 guard-cell, 228, 230  
 gum, 78  
 gut, 4  
*Gymnocalycium hossei*, 5  
 gymnosperm, 11, 168, 176, 202, 260,  
   261, 266  
 gynæcium, 295, 296, 298  
  
 hair, 50, 60, 64, 134, 310, 311  
   glandular, 197  
 hairiness, 223  
 haustorium, 313, 367  
 heartwood, 3, 72, 271  
 heat, 7, 20, 67, 69, 92, 287, 316, 344  
   sterilisation, 352, 354, 367  
 height, 329  
*Helianthus annuus*, 233–238, 243, 265  
 hemicellulose, 77, 209

- Hemileia vastatrix*, 366
- heredity, 324-334
- heterosis, 331
- heterosporous, 161
- heterothallism, 365
- hexa-amylose, 77
- hexose, 74, 92
- hexosediphosphate, 89, 342
- Hofmeister, 293
- holdfast, 114, 126, 129
- hook, 312, 313
- Hooke, 46
- hops, 344
- hordenine, 94
- hormone, 81, 217, 284
- horse-chestnut, 260-263, 292
- horsetail, 12, 160
- humus, 354, 370
- Hyalosphenia lata*, 29
- hybrid, 328
- hybrid vigour, 331, 344
- hybridisation, 330, 338
- hydrogen, 35, 72, 89
  - acceptor, 90
  - carrier, 89
  - ion, 82
- hydrosol, 37
- hypha, 362, 371
- hypocotyl, 182, 317-319
- hypodermis, 249, 253
- imbibition, 37
- inbreeding, 330
- Indian ink, 34
- Indian shot, 317
- Indigofera gerardiana*, 286
- individual, 192
- $\beta$ -indolylacetic acid, 284
- indusium, 153, 154
- inflorescence, 277, 292-294, 309
  - bud, 260
  - scar, 262
- inhibition, 284
- insect, 321
- insect pollination, 294-297
- insectivorous plant, 5
- integration, 44, 192
- integument, 171, 176, 301, 307
- intercellular space, 44, 224, 226, 247, 250
- intercellular substance, 44
- intermediate, 87
- internode, 186, 233, 239, 262
- inulin, 78
- invertase, 83, 316
- iodine, 42, 77, 80
- ion, 31, 36, 80, 256
- Iris*, 185, 252
- iron, 256
- irritability, 2, 20, 27, 285-290
- isogamete, 102, 121
- isogamy, 121
- Janus green, 41
- juniper, 168, 260, 315
- kelp, 149
- lactic acid, 89, 350
  - dehydrogenase, 89
- lamina, 221-223, 238
- Laminaria*, 149
- larch, 168, 261
- Latin, 11
- lattice, 200
- leaf, 3, 5, 61, 65, 151, 221-231, 287, 290
  - form, 221-223
  - movements, 287
  - scar, 262
  - structure, 223-229
- leaf-base, 151
- leaflet, 151, 286
- leaf-stalk, 152, 221
- legume, 308
- Leguminosae, 335
- lenticel, 263, 274
- lentil, 320
- Lepiota procera*, 14
- leptotene, 332
- leucoplast, 68
- Libocedrus decurrens*, 11
- Licea pannorum*, 29
- lichen, 13
- life, 7, 69
- light, 7, 65-69, 228
  - response, 27, 183, 222, 286, 289, 318
  - stimulus, 99, 287
- lignification, 209
- lignin, 86, 209
- Ligustrum vulgare*, 213
- lilac, 264
- lily, 192, 239, 300, 302, 304, 306
- lime, 260, 263
- liming, 367
- linen, 78, 207
- linkage, 325, 330, 334
- Linnæus, 10
- Linna borealis*, 10
- lipase, 83, 88, 316
- lipoprotein, 81
- liverwort, 12, 13, 140-146
  - leafy, 146
- living, 1, 4, 14
- locomotion, 6, 13
- loss of vigour, 360
- Lunularia*, 13, 193
- Lycopodon perlatum*, 14
- Lycopodiales, 160
- Lycopodium*, 161
- Macrocystis*, 124
- magnesium, 42, 256
- magnitudes, 35
- maidenhair tree, 168, 177
- maize, 238-243, 281, 320, 330



- making do, 139  
 male fern, 151-159  
 malt, 76, 344  
 maltase, 83  
 malting, 344  
 maltose, 76  
 mammal, 9  
 manganese, 257  
 marrow seedling, 318  
 maturation, 2  
 meadow rue, 297  
 medulla, 126, 127  
 medullary ray, 235, 265  
 megasporangium, 165, 172, 300  
 megaspore, 161, 165, 293, 300-302  
 megasporophyll, 168, 171  
 meiosis, 148-150, 170, 300, 332-334  
 membrane, 38  
   nuclear, 49  
   semipermeable, 58, 255  
 Mendel, 325-331  
 Mendelian ratios, 326-330  
 Mendel's hypothesis, 325  
 meristem, 47, 48, 215, 246, 264, 282  
 mesocarp, 310  
 mesophyll, 162, 224-227, 229  
 metabolism, 85-88, 349  
 metabolite, 42, 79  
 metaphase, 53, 332  
   plate, 55  
 metaphloem, 237, 241  
 metaxylem, 237, 241, 253  
 micelle, 37, 58, 78  
 micro-nutrient, 256  
 micro-organism, 69  
 micron ( $\mu$ ), 17, 35  
 micropyle, 172, 301, 302  
 microscope, 14, 34  
   electron, 34  
   phase contrast, 51  
 microsporangium, 163, 169, 294-300  
 microspore, 161-166, 170, 293, 296-300  
 microsporophyll, 169  
 middle lamella, 46, 57, 117, 128, 209, 273, 276  
 midrib, 126, 146, 162, 221, 237  
 migration, 139  
 mildew, 13, 367  
 millimicron ( $m\mu$ ), 32, 35  
 mineral, 1  
*Mirabilis jalapa*, 326  
 mistletoe, 313  
 mitochondria, 41  
 mitosis, 51-56, 175, 333  
   anaphase, 55  
   metaphase, 53-55  
   metaphase plate, 55  
   prophase, 51  
   telophase, 55  
 Muhl, von, 46  
 molecule, 31, 36, 37, 38, 73  
 molybdenum, 257  
 monocotyledon, 182, 217, 221, 238, 252  
 monopodium, 184, 185, 261, 292  
 monosaccharide, 74  
 moss, 12, 146  
 motility, 4  
 mould, 13, 91, 363-365  
 movement, 18, 23  
 mucilage, 37, 78, 100, 128, 134, 144, 157  
   envelope, 105, 108  
   formation, 210  
   surface, 117, 125  
*Mucor*, 363-365  
 mulberry, 310, 311  
 multiplication, 191  
 muscle, 44, 45  
 mushroom, 13  
 mutant, 337  
 mutation, 337  
 mycelium, 362, 367  
 mycorrhiza, 369-372  
   ectotrophic, 369  
   endotrophic, 370  
 Myxomycete, 43, 286  
  
 nastic movement, 286  
 nectar, 197, 295  
 nectary, 44, 197, 295  
   extrafloral, 211  
*Nepenthes*, 5, 198  
*Nereocystis*, 124  
 nitrate, 86, 256, 354  
 nitrification, 354  
*Nitrobacter*, 354, 356  
 nitrogen, 72, 256, 283  
   cycle, 356  
   fixation, 354, 371  
*Nitrosomonas*, 347, 354, 356  
 node, 181, 186, 237, 263  
 nodule, 355  
 nomenclature, 9  
 non-living, 1, 14  
 nucellus, 172, 301, 306  
 nuclear division, 51-56  
 nuclear membrane, 49  
 nuclear sap, 51  
 nucleic acid, 49  
 nucleolus, 23, 49  
 nucleoprotein, 81  
 nucleus, 18, 23, 41, 48-56, 98, 116, 148, 156, 174, 197, 301-304, 332, 340  
 nut, 307, 317  
 nutrition, 6, 19, 22, 26, 283  
   holophytic, 26, 99  
   holozoic, 26  
   saprophytic, 26  
  
 oak, 276, 292, 299  
 oat, 315, 320

- Oenothera*, 287, 338  
 offset, 182  
 oil, 69, 78, 88, 321  
     globules, 18  
 oogamy, 122  
 oogonium, 131, 132, 369  
*Opuntia cylindrica*, 5  
 orange, 308  
 orchid mycorrhiza, 370  
 organic carbon, 69  
 organic substance, 4, 7, 72-83  
 organisation, 4, 13, 176, 192  
 organism, 1, 44  
 osmosis, 20, 27, 58, 230  
 osmotic pressure, 20, 59, 228  
 ovary, 300, 307-310  
 ovule, 171, 172, 300-302  
 oxidase, 83, 89  
 oxidation, 89  
 oxygen, 19, 46, 316, 352  
     debt, 24  
     photosynthetic, 68  
     respiratory, 88-92  
  
 pachytene, 332  
 palisade, 126, 224, 226  
 palm, 321  
 palmella, 98, 100  
 palmitin, 79  
*Pandorina*, 35, 103-105, 121  
     cænobium, 104  
     reproduction, 103  
 paper, 78, 207  
 pappus, 311  
 paramylum, 23  
 parasite, 4, 340, 365  
     complete, 357  
     facultative, 366  
     obligate, 366  
     partial, 357  
 parasitism, 362  
 parchment, 38, 59  
 parenchyma, 46, 57, 237, 241, 251, 254, 267  
 parent, 324-331  
 parthenospores, 119  
 particle, 33-39  
     colloidal, 33  
     microscopic, 34, 35  
     submicroscopic, 34, 35  
     ultramicroscopic, 34, 35  
 pea, 319, 327-330  
 peat, 354  
 pectic acid, 276  
     material, 57, 209, 249  
     substance, 78, 86  
*Pellia*, 54, 140-146  
     growth, 141  
     reproduction, 141, 142  
     sporogonium, 144, 145  
     structure, 140, 141  
  
*Pellia neesiana*, 142  
 penicillin, 353, 373  
*Penicillium notatum*, 373  
*Penstemon*, 335  
 pentose, 74  
 peptide, 80  
*Peranema trichophorum*, 25  
 perennation, 191  
 perennial, 179, 182-194, 281  
 perianth, 295, 298, 309, 311  
 periblem, 246  
 pericarp, 307-313  
 pericycle, 236, 243, 250-252, 266, 278  
     fibres, 236, 267  
 perisperm, 176, 306  
*Peronospora*, 367-369  
 petal, 182, 295  
 petiole, 221, 237, 276, 335  
 phæoplast, 124, 127, 133  
 phase, 32, 42  
 phelloderm, 273  
 phellogen, 266, 273-275, 278  
 phenotype, 122  
 phloem, 203, 225, 236, 250, 267, 278, 279  
*Phoma*, 371  
 phosphate, 73, 89, 93, 256, 342  
 phosphorus, 256  
 phosphorylase, 77  
 phosphorylation, 90  
 photocatalyst, 66  
 photo-electric cell, 2  
 photonastic movement, 287  
 photoperiod, 282  
 photosensitiser, 66  
 photosynthesis, 4, 64-69, 88, 127, 356  
     bacterial, 347  
     combination stage, 67  
     dark stage, 68  
     diffusion stage, 67  
     photostage, 68  
     products, 68  
     significance, 69  
 phototropism, 289  
 phyllode, 335, 336  
 phylum, 11  
*Phytophthora infestans*, 366  
 pigment, 13, 27, 64, 81, 124, 326  
 piliferous layer, 249  
 pine, 11  
 pineapple, 309  
 pinna, 151  
 pinnule, 151  
*Pinus*, 149, 168-176, 208  
     cones, 169, 171, 172  
     fertilisation, 174, 175  
     gametophyte, 170, 173  
     mycorrhiza, 370  
     pollination, 172  
     seed, 175  
     short shoot, 264

- Pinus sylvestris*, 11, 168, 172  
 pit, 58, 200, 207  
   bordered, 207, 267  
   membrane, 207  
   simple, 207  
 pitcher plant, 5  
 pith, 218, 238, 253  
 plankton, 95  
 plant, 1, 3, 6-14, 69  
   acids, 42, 88, 91  
   autotrophic, 64  
   cushion, 179, 180  
   exposed, 179  
   green, 4, 372  
   heterotrophic, 64, 85, 362  
   hidden, 179, 180  
   hygiene, 366  
   land, 139, 149  
   long day, 283  
   monocarpic, 178  
   nutrient, 85, 256  
   oxidations, 89  
   polycarpic, 178  
   rosette, 180  
   shade, 229  
   short day, 283  
   succulent, 91, 198  
   surface, 179, 180  
   world, 11  
 plasmagel, 18  
 plasmalemma, 18  
 plasmasol, 18  
 plasmodium, 29  
 plasmolysis, 49, 60, 202, 251  
   threshold, 60  
*Platyserium*, 12  
*Pleodorina*, 35, 106  
*Pleodorina californica*, 106  
*Pleodorina sphaerica*, 106  
 plerome, 247  
*Pleurococcus vulgaris*, 21  
 plum, 308, 310  
 plumule, 304, 306  
 pod, 307  
 poison, 19  
 pollard, 272  
 pollen, 170, 293, 296-300, 332  
   grain, 49, 170, 299, 303  
   mother cell, 332  
   sac, 296-300  
   tube, 174, 176, 303  
 pollination, 172, 294-298  
 polypeptidase, 83  
 polypeptide, 80  
*Polypodium irioides*, 12  
 polysaccharide, 42, 74, 76-78  
 pome, 309, 310  
 population, 44  
 potassium, 73, 256  
 potato, 88, 186-188  
   blight, 366  
   virus disease, 360  
*Potentilla reptans*, 183  
 prickles, 8  
 prickly pear, 322  
 primordium, 213, 216, 217, 238  
 privet, 213  
 procambial strand, 265, 277, 317  
 procambium, 247  
 progeny, 324-331  
 prolamin, 81  
 prophase, 51, 332  
 protandry, 296  
 protection, 179  
 protein, 19, 36, 65, 79-82, 86, 144, 256,  
   279, 354  
   gel, 37  
   molecule, 42, 53, 79  
   protoplasmic, 317  
   reagent, 80  
   reserve, 316, 321  
   respired, 93  
   sol, 33  
 proteinase, 82, 83  
 prothallial cell, 164, 170  
 prothallus, 155, 160, 165  
 Protista, 13, 99  
*Protococcus*, 13, 21-22, 28, 35, 41  
   excretion, 22  
   nutrition, 22  
   reproduction, 22  
*Protococcus viridis*, 22  
 protogyny, 298  
 protophloem, 219, 237, 240  
 protoplasm, 3, 17, 22, 41, 92, 201, 267,  
   316, 346  
   secretory, 197  
 protoplasmic bridges, 115, 116  
   colloid, 36  
   constituents, 73  
   fats, 79  
   fibrils, 2, 3, 44, 99  
   immortality, 97  
   proteins, 79  
 protoplast, 118  
 protoxylem, 219, 237, 241, 247, 250,  
   253, 278  
 Protozoa, 49  
 pruning, 264  
 pseudopodium, 18  
*Pseudotsuga douglasii*, 11  
*Pteridium aquilinum*, 160, 185, 201  
 Pteridophyta, 12, 160, 335  
 Pteridosperms, 12, 177  
*Puccinia*, 366  
 pulvinus, 287  
 pure line, 330  
 putrefaction, 69, 353  
 pyrenoid, 98, 103, 108, 114, 116  
 pyruvic acid, 83, 87, 90, 93  
*Pythium*, 366  
*Quercus suber*, 275  
 quinine, 372

- raceme, 292, 293
- radicle, 304, 306, 317-319
- Ranales, 10
- Ranunculaceæ, 297, 334
- Ranunculus acris*, 292, 294-297
- Ranunculus ficaria*, 258
- Ranunculus repens*, 183, 248-251
- raphanin, 372
- raspberry, 8, 9
- ray, 237, 265, 268, 271, 278
  - initial, 272
- reagents, 375
- receptacle, 143, 294, 295, 309, 311
- reproduction, 2, 97, 178
  - Amæba*, 21
  - bacteria, 350
  - Chlamydomonas*, 100-103
  - Dryopteris*, 153-157
  - Eudorina*, 106
  - Euglena*, 25, 27
  - Flowering Plants, 292 *et seq.*
  - Fucus*, 130-135
  - Mucor*, 363-365
  - Pandorina*, 103-105
  - Pellia*, 141-146
  - Peronospora*, 368
  - Pinus*, 168-176
  - Protococcus*, 22
  - Selaginella*, 163-166
  - Spirogyra*, 117-121
  - Ulothrix*, 114
  - Virus, 358
  - Volvox*, 109-112
  - Yeast, 343
- reserve, 7, 87, 179, 316
- resin, 173, 197, 261
- respiration, 2, 20, 24, 44, 69, 88-93
  - aerobic, 89, 256, 286
  - anaerobic, 90
  - animal, 93
  - fatty tissues, 91
  - plant, 93
  - poison, 19
  - succulents, 91
- respiratory quotient (R.Q.), 91
- resting stage, 115, 118, 351, 365
- rhizoid, 135, 140, 141, 146, 155, 165
- rhizome, 151, 153, 180, 183-186, 191
- rhizophore, 161, 167
- Rhizopus nigricans*, 365
- rice, 316, 320
- ring, annual, 269
  - scar, 262-264
- root, 162, 245-253, 277, 285, 288
  - adventitious, 151, 180-192, 284
  - cap, 246, 252, 317
  - contractile, 189
  - growing point, 245, 289
  - hair, 49, 247, 248, 254, 355
  - lateral, 251
  - pressure, 255
  - prop, 256
- root (*continued*)
  - stock, 180
  - structure, 246-253
  - system, 245, 254, 281
  - tap, 181, 245, 257, 258
  - tip, 247, 256
  - tuber, 255, 258
- Rosa eglanteria*, 10
- Rosaceæ, 10
- Rosales, 10
- rose hip, 311
- Rubus fruticosus*, 8, 10
- Rubus idæus*, 9, 10
- runner, 182, 183, 191
- rye, 282, 320
- Saccharomyces*, 343
- Saccharomycetes*, 340
- salt, 59
- salts, 4, 37, 42, 85, 99, 140, 255
- Sambucus nigra*, 260
- saprophyte, 340
- sapwood, 271
- Sarothamnus scoparius*, 308
- scale (leaf), 184-191
- schizocarp, 313
- scutellum, 319, 320
- sea, 13
- sea lettuce, 124
- sea water, 20
- sea wrack, 124
- seaweed, 37, 64, 86, 113, 124, 149
- secondary rays, 267, 271
- secondary thickening, 266-278
- sections, 126
- sedimentation, 33
- seed, 11, 179, 304, 306, 329
  - coat, 317
  - dispersal, 310
  - dormant, 2, 315
  - gels, 37
  - germinating, 315
  - habit, 176
  - leaf, 176
  - Pinus*, 175
  - plant, 11, 12, 168 *et seq.*
  - reserve, 79, 81, 88
  - respiration, 91
- seedling, 176, 183, 317-321, 335
- segregation, 325
- Selaginella*, 12, 149, 161-167
  - cone, 163
  - fertilisation, 165
  - gametophytes, 164-165
  - habit, 161
  - sporangia, 163-165
- Selaginella kraussiana*, 161, 167
- Selaginella martensii*, 165
- Selaginella selaginoides*, 161
- selection, 121, 336
  - natural, 338

- self-pollination, 330  
 sepal, 182, 295, 298  
 sex, 101-122  
 sexual differentiation, 120  
 sexual reproduction, 120  
   survival of, 339  
 sexuality, 118  
 shive, 276  
 shoot, 8, 9, 181, 184  
   development, 317-320  
   growing point, 213  
   lateral, 181, 264  
   short, 262, 264  
 shrub, 179, 182, 260  
 sieve plate, 200, 241, 279  
 sieve tube, 152, 200-203, 225, 237,  
   241, 251, 267, 268, 279  
 silicon, 72  
 silt, 31  
 skeleton, 3, 46, 78, 272  
 sleep movement, 287  
 slime fungus, 43, 286  
 slime strand, 202  
 soil, 4, 31, 180, 253  
   acid, 370  
   bacteria, 355  
   fertility, 355, 367  
   particle, 248  
   solution, 4, 245, 255  
 sol, 31-38, 41  
   lyophilic, 33, 36  
   lyophobic, 33, 36  
 solute, 31, 38, 59  
 solution, 3, 31, 59  
   hypertonic, 60  
 soma, 97-113, 139, 170, 178  
 sorus, 153  
 soya, 320  
 specialisation, 44, 192  
 species, 9, 353  
 spectrum, 65  
 sperm, 107, 111, 120, 133, 142, 143,  
   150, 156, 157, 161, 164, 170, 174,  
   302, 304  
   mother cell, 302  
 Spermaphyta, 11  
*Sphaerella lacustris*, 99  
 spike, 292, 293  
 spindle, 53-57, 117, 333  
 spine, 224  
 spirillum, 346  
 spirits, 344  
*Spirochæte pallida*, 347, 357  
*Spirogyra*, 13, 57, 96, 112, 115-119,  
   121, 149  
   reproduction, 116-119  
*Spirogyra longata*, 120  
*Spirogyra maluscula*, 57  
*Spirogyra setiformis*, 120  
 sporangium, 149, 154, 163, 364  
 spore, 12, 37, 113, 145, 149, 153, 163,  
   293, 343, 350, 363  
 spore (*continued*)  
   capsule, 145, 150  
   mother cell, 149, 163  
 sporogonium, 144, 145, 147, 163  
 sporophyll, 163, 182  
 sporophyte, 149-155, 168  
 sport, 337  
 spraying, 367  
 spreading, 191  
 spur, 262, 264  
*Stachys tuberifera*, 186  
 stamen, 182, 295-300, 309, 355  
 staminode, 335  
 staphylococcus, 347  
 starch, 76, 267  
   chloroplast, 68  
   grain, 76, 81, 228, 250, 270  
   guard cell, 228  
   pyrenoid, 116  
   reserve, 188, 198, 316, 320  
   sheath, 235  
   soluble, 35  
 stele, 250, 252  
 stem, 61, 181, 233-243, 288  
   apex, 215  
 sterilisation, 352  
*Stigeoclonium*, 96  
 stigma (eye spot), 23, 99  
 stigma (floral), 296, 303  
 stimulus, 7, 20, 285-290  
 stipe, 126, 129  
 stoma, 162, 227-230, 233, 274, 335,  
   368  
 stomatal pore, 228, 230  
 stomium, 154  
 stone, 309  
   fruit, 308  
 strawberry, 183, 310, 311  
 streptococcus, 347  
 strobilus, 160  
 structure, 6, 11, 44, 121  
 style, 296, 303, 311  
 suberin, 79, 210, 273  
 suberisation, 210  
 succulence, 334  
 succulent leaves, 223, 224  
   respiration, 91  
 sucker, 261  
 sucrose, 38, 68, 76, 88  
 suction pressure, 59, 254  
 Sudan III, 79  
 sugar, 32, 68, 74-76, 85, 88, 316  
   breakdown, 90  
   translocation, 227, 278  
   vacuolar, 247  
 sulphate, 256  
 sulphur, 72, 256, 347  
   bacteria, 347  
 sulphuretted hydrogen, 347  
 sun, 69  
 sundew, 5  
 sunflower, 233-238, 265

sunlight, 7  
 sterilisation, 352  
 surface, 34, 67  
     colloidal, 34-36  
     energy, 35  
     specific, 35  
     tension, 35, 36  
 suspension, 31  
 suspensoid, 32  
 suture, 308  
 sweet briar, 9  
 sycamore, 260, 263, 266-273, 310, 312  
 symbiosis, 355, 362  
 symplast, 3  
 sympodium, 184, 264, 292  
 synergid, 301  
 synthesis, 85-87, 92  
*Syringa vulgaris*, 264  
  
 tannin, 81  
 tapetum, 164, 169, 299  
 tapeworm, 4  
 taxis, 286  
*Taxodium distichum*, 168  
 telophase, 55  
 temperature, 19, 20, 24, 37, 38, 67, 230, 282, 316, 350  
 temperature, effect on, bacteria, 350  
     diffusion, 38  
     evaporation, 230  
     gels, 37  
     germination, 316  
     irritability, 20  
     movement, 19, 24  
     photosynthesis, 67  
     vernalisation, 282  
 tendril, 224  
 tensile strength, 243, 254  
 testa, 304, 307, 309, 317-319  
 tetrad, 148, 163, 170, 299, 300, 332  
 tetraspore, 151  
*Thalictrum minus*, 297  
 thallus, 13, 125-129, 140  
 thiol, 256  
 Thiorhodaceæ, 347  
 thornapple, 313  
*Tilia*, 260  
*Tilia cordata*, 263  
 tissue, 44, 197, 233  
     mechanical, 264  
 toadstool, 13  
 tomato, 308  
*Torula*, 345  
 torus, 208  
 toxin, 339, 350, 357  
 tracer, 68  
 tracheid, 152, 153, 204, 225, 241, 251, 254  
 translocation, 278  
 transpiration, 229-231, 253-255  
     stream, 231

tree, 1, 12, 168, 179, 182, 260-279  
     trunk, 3, 206, 264, 274  
 triolein, 79  
 tropism, 288-290  
 tuber, 86, 186-188, 191  
     root, 258  
 tulip, 191, 287  
*Tulipa clusiana*, 324  
 turgor, 61, 228, 242, 287  
     pressure, 59  
 turnip, 179  
 twig, 261-264, 276  
 Tyndall effect, 34  
  
*Ulothrix*, 13, 96, 113-115, 149  
*Ulothrix zonata*, 113  
 ultramicroscope, 41  
*Ulva lactuca*, 124  
 unicells, 28, 29, 42  
 urea, 89  
 uric acid, 20  
  
 vaccination, 357  
 vacuolation, 47, 204, 247  
 vacuole, 34, 47, 59, 115, 129, 198-200, 341  
     cœnocytic, 43, 363  
     contractile, 20, 23, 27, 98, 118  
*Valonia*, 43  
 variation, 325, 334  
 varieties, 10, 324-330  
     establishment, 339  
     origin, 337  
 vascular bundle, 224, 233-243, 263  
     cylinder, 235, 251  
 vegetative propagation, 160, 192, 324, 360  
 vein, 222  
 venation, 222  
 venter, 143, 144, 156, 158  
 vernalisation, 282  
 vessel, 205, 225, 237, 241, 251, 254, 267-271  
 vestige, 334  
 viability, 315  
*Victoria regia*, 42  
 vinegar, 350  
 virus, 13, 35, 358-360  
     tobacco, 359  
 vitamin, 81, 345, 372  
*Volvox*, 13, 96, 108-112, 149  
     reproduction, 109  
*Volvox aureus*, 35, 107-110  
  
 wall pressure, 59  
 water, 19, 36, 64, 73, 140, 167, 315  
     absorption, 253  
     culture, 257, 259  
     deficit, 254  
     dispersal of seeds, 313  
     molecule, 31, 256

- water (*continued*)
  - transpired, 229
  - vapour, 46, 229
- water-lily, 42
- weed, 185
- weed-killer, 285
- wheat, 37, 253, 315
- willow, 272
- wilting, 230
- wind, 230, 297, 310
  - pollination, 297-299
- wine making, 344
- wing, 310-312
- winter, 179
  - twig, 261-264
- wood, 1, 47, 209, 266-272
- work, 92
- xanthophyll, 124
- xylem, 152, 225, 236-242, 250, 253, 267-272
  - mother cells, 267, 268
- yeast, 13, 35, 340-345
  - cell, 340, 341
  - life cycle, 343, 344
  - metabolism, 342
  - nutrition, 341
  - respiration, 342
  - sexual fusion, 343
  - spore formation, 343
- yew, 168
- Zea mais*, 238-243
- zooglæa, 346
- zoospore, 105, 108, 112, 114
- Zygnema*, 121
- zygosis, 148
- zygote, 101, 105, 108, 111, 115, 118-120, 135, 144, 149, 157, 166, 304, 364, 369
- zygotene, 332
- zymase, 342, 345
- zymohexase, 83, 89, 342







